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Human-Managed vs. Natural Grazing Systems: Exploring Effects of Livestock and Wildlife Grazing at Multiple Scales

Megan Esther McSherry
Syracuse University

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Human-Managed vs. Natural Grazing Systems: Exploring Effects of Livestock and Wildlife Grazing at Multiple Scales

ABSTRACT

Grazing by large herbivores is the most prevalent land use on grassland ecosystems, which cover greater than 40% of the earth's land surface and provide critical ecological and economic benefits. As such, understanding how grazing impacts different aspects of the ecosystem is of especially great importance. This study uses a range of approaches to explore the potentially contrasting effects of grazing across human-managed, livestock-grazed systems and natural, wildlife-grazed systems. The first chapter uses a short-term, small-scale approach in assessing differences across management type in plant community composition following a relaxation of grazing. Results reveal that livestock and wildlife grazers may not be functionally different, but rather exhibit different effects due to the way they are managed (free-ranging vs. herded, etc. which affects grazing pressure and its spatial and temporal distribution). The second study explores how herders make livestock movement decisions and reveals that while individual variation in herd movement decisions is related to factors such as herd size, purpose for keeping livestock, and number of herders, the chief drivers influencing herd movement seem to be limited available grazing space and a lack of options. The third study uncovers global patterns regarding environmental and other influences on grazer effects on soil carbon storage. And finally, the last chapter synthesizes these results and suggests recommendations for policy and management. These results have implications for rangeland and wildlife management as well as future ecological studies.

HUMAN-MANAGED VS. NATURAL GRAZING SYSTEMS: EXPLORING EFFECTS OF LIVESTOCK AND WILDLIFE GRAZING AT MULTIPLE SCALES

by

Megan E. McSherry

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TABLE OF CONTENTS

LIST OF ILLUSTRATIVE MATERIALS

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

SUPPLEMENTAL INFORMATION

CHAPTER 1

Introduction and context

Grazing by large ungulates is the most prevalent land use on grasslands and other rangelands, which cover more than 40% of the earth's terrestrial surface and are found in nearly every region in the world (Oenema *et al.* 1997; Sanderson *et al.* 2004; Derner & Schuman 2007a). In addition to being ubiquitous, large ungulate grazing is of enormous importance- both economically, to the > 1 billion people whose livelihood comes from domestic livestock (FAO 2006) and to the hundreds of national parks and reserves across the world that feature grazing animals for tourism services; and ecologically, as large herbivore grazing can influence ecosystem functioning through its impacts on a wide variety of ecosystem properties including, but not limited to, primary production (McNaughton 1976; Frank & McNaughton 1993; Milchunas & Lauenroth 1993; Noy-Meir 1993; Oba *et al.* 2000), plant community composition (Vinton *et al.* 1993; Hartnett *et al.* 1996; Augustine & McNaughton 1998; Hickman *et al.* 2004; Cingolani *et al.* 2005; Hendricks *et al.* 2005), and rates of nutrient cycling (Bryant *et al.* 1983; Ruess & McNaughton 1987; Seagle *et al.* 1992; Hobbs 1996; McNaughton *et al.* 1997; Anderson *et al.* 2006). Grazing systems also have high conservation importance as they have the unique ability to support extremely high densities of herbivores (Frank *et al.* 1998) as well as high levels of biodiversity among ungulates and other taxonomic groups. For these reasons, it is imperative to understand the different ways in which grazing can shape an ecosystem and what other factors influence these effects.

The influence of herbivore type or management, *i.e.* whether a system is managed for native wildlife or for domestic livestock, on grazing effects is one factor that has not yet been widely explored despite the potential influence it could have on the magnitude and direction of grazing effects. Thus, this study aims to explore differences in effects of grazing between natural, wildlife-grazed systems and human-managed, livestock-grazed systems. A central question is: what are the effects of grazing and what differences in grazing impacts, if any, exist across natural and human-managed systems? Lastly, how do grazing impacts affect the resilience of the grazing system as a whole?

In an attempt to understand grazing effects on ecosystem-level resilience, this study utilizes an interdisciplinary approach to explore effects at different spatial scales, starting at the fine-scale plot level and working up to the global scale. I begin in the second chapter with a short-term, small-scale ecological study that compares native wildlife and domestic livestock grazing effects on plot-level plant community composition. Recent research has shown that many effects on nutrient cycling and plant productivity, as well as on carbon sequestration, are closely related to shifts in plant community composition caused by herbivores (Pastor & Cohen 1997; Augustine & McNaughton 1998; Hickman *et al.* 2004; Bagchi & Ritchie 2010) and thus, understanding how native and domestic grazers modify plant community composition over time may reveal possible mechanisms by which they have potentially contrasting effects on ecosystem function and sustainability. This study, which was completed within two regions of the famed Serengeti ecosystem of northern Tanzania, explores the functional similarity of native and domestic herbivores and tests the hypotheses that (1) past grazing by the two groups has led to different plant communities, and (2) relaxation of grazing in native and domestic systems will cause plant composition of the two systems to diverge, or to become more different from each other than initially, potentially exhibiting trajectories to different community states (Schacht 1993; van de Koppel *et al.* 1997; Bestelmeyer *et al.* 2003; Stringham *et al.* 2003). Finally, this study explores the effect of grazing intensity on herbivore effects on composition in order to further disentangle potential differences across management type.

In the third chapter, I dig deeper into understanding impacts of domestic grazers in particular, by widening the lens to the level of the perspective of an individual livestock owner and taking a sociological approach to investigate factors that influence decisions on herd movement and management. Domestic livestock-grazed systems differ from natural grazing systems in that individual animals and herds are not free-ranging and instead, movement decisions are made by human managers. That domestic grazers exhibit reduced mobility and tend not to engage in migratory behavior similar to native wildlife has been suggested as a potential reason why grazing by native herbivores positively affects ecosystem properties while grazing by domestic stock may not (McNaughton 1984, 1986, 1993). Thus, how domestic herd movement decisions are made and the socioeconomic and other factors that influence or constrain them are a significant piece to the 'grazing impact' puzzle because of the effect they can have on the spatial distribution of grazer impacts across the landscape (Illius & O'Connor 1999). This study uses questionnaires to learn what environmental and socioeconomic factors influence individual herd movement decisions and to explore limitations to movement options, such as areas where livestock are prohibited due to land being used for agriculture or for wildlife conservation. This study was carried out in the same two regions as the above ecological experiment in order to facilitate comparison across regions and to make potential connections between herding strategies and grazing effects on plant community compositional shifts.

The fourth chapter pans out to take the broadest perspective on grazing effects in a global meta-analysis of grazer effects on soil organic carbon (SOC). While the second chapter explored in-depth one potential mechanism through which grazers can affect soil carbon storage (*i.e.* through changes in plant species composition (Bagchi & Ritchie 2010)), this analysis tests specific hypotheses on how various environmental (soil type and mean annual precipitation), biotic (grazing intensity and dominant grass type), and study design (soil sampling depth and study duration) factors might influence variation in grazer effects on SOC density. Unfortunately, the dearth of studies in the literature that explored effects of native grazers on SOC made it impossible to include the effects of herbivore type in the analysis. Nonetheless, this meta-analysis of studies across the globe reveals interesting patterns in grazer effects on SOC while highlighting the importance of local environmental context in predicting grazer effects.

Finally, the fifth chapter synthesizes the information presented in the preceding chapters and makes connections between the various projects and across the different scales. In this chapter, I hope to convince the reader of the need for acknowledging the socioeconomic and cultural context of ecological problems and of the value of utilizing an interdisciplinary toolbox in tackling ecological questions, particularly questions centered in human-natural systems, such as grazing systems. Lastly, this chapter discusses some important implications for management and suggests a few key policy recommendations.

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CHAPTER 2

Human-managed vs. natural systems: comparing effects of relaxing grazing on plant species composition

ABSTRACT

Grazing by large ungulates is the most prevalent land use on grasslands and other rangelands, which cover more than 40% of the earth's land surface (Oenema *et al.* 1997; Sanderson *et al.* 2004). While grasslands often support extremely high densities and species diversity of native herbivores (Frank *et al.* 1998), the current major use of grasslands for domestic livestock grazing (Skarpe 1991) has led to apparent overgrazing and degradation of rangelands (McNaughton 1993; Painter & Belsky 1993). While many studies have been done to assess the various impacts of grazing, very few have compared these impacts by herbivore type. This study explores the functional similarity (or dissimilarity) of native and domestic herbivores by comparing plant community shifts following relaxation of grazing across paired livestock-grazed and wildlife-grazed sites in the Serengeti ecosystem of Tanzania. The hypotheses that (1) past grazing has led to very different plant communities, and (2) relaxation of grazing in native and domestic systems will cause plant composition of the two systems to diverge, potentially exhibiting trajectories to different community states (Schacht 1993; van de Koppel *et al.* 1997; Bestelmeyer *et al.* 2003; Stringham *et al.* 2003), were tested using a grazing exclosure experiment at four pairs of livestock-grazed and wildlife-grazed sites that shared similar environmental and edaphic characteristics. By fencing a series of plots for graduated amounts of time, the effect of plot grazing intensity was also tested. Results show that while regional differences and site history strongly influence the magnitude of compositional change, overall, relaxing grazing did not lead to divergence in composition across management types. Rather, despite significant differences in the magnitude and/or direction of shifts in grass, forb, and sedge relative abundance and differing trajectories of some key species, livestock-grazed and wildlife-grazed plots exhibited a convergence in compositional similarity across wet seasons. These results suggest that differences in impacts across livestock-grazed and wildlife-grazed systems may be due more to aspects of management, including spatial and temporal patterns of grazing (Ellis & Swift 1988; Illius & O'Connor 1999), than to functional differences in herbivore type.

INTRODUCTION

Grazing by large ungulates is the most prevalent land use on grasslands and other rangelands, which cover more than 40% of the earth's land surface (Oenema *et al.* 1997; Sanderson *et al.* 2004). Grasslands often support extremely high densities and species diversity of herbivores (Frank *et al.* 1998), which may reflect a long (> 1 My) coevolutionary history between wild ungulate grazers and native herbaceous plants that has allowed their coexistence (Frank *et al.* 1998). However, the current major use of grasslands across the globe is for domestic livestock grazing (Skarpe 1991), a practice that has largely replaced natural co-evolved grazing systems. In Africa alone, pastoralism accounts for the use of almost 40% of land across the continent (van Cotthem 2007). Although some pastoralist systems have persisted for thousands of years, recent increases in populations and more sedentary lifestyles of pastoralists (Galvin *et al.* 2008), accompanied by increases in livestock numbers, have led to apparent overgrazing and degradation of rangelands (McNaughton 1993; Painter & Belsky 1993). Therefore, a vital question is how strong are grazing impacts of large herbivores and how resilient are plant communities to a reduction in or absence of grazing in native versus domestic grassland systems.

While many studies have looked at effects of grazers on plant community composition and on species richness and diversity (Vinton *et al.* 1993; Hartnett *et al.* 1996; Augustine & McNaughton 1998; Hickman & Hartnett 2002; Hickman *et al.* 2004; Cingolani *et al.* 2005; Hendricks *et al.* 2005; del Pozo *et al.* 2009), very few studies have compared impacts of grazing between native and domestic grazers and until recently (Bagchi & Ritchie 2010), those that did (Damhoureyeh & Hartnett 1997; Towne *et al.* 2005) compared only effects of a single species of domestic and native grazer alone and were done in controlled, experimental settings rather than in natural habitats. Thus, there is need for studies that compare the impacts of grazing by multi-species assemblages of domestic versus native ungulates on plant community composition within a coupled human-natural grazing ecosystem. Such studies may determine the functional similarity (or dissimilarity) of two types of systems of multiple grazing species on plant communities. Specifically, an important research goal is to determine whether the relaxation of grazing in natural and managed systems produces similar or different shifts in plant community composition.

The impacts of different types of grazing systems (native-coevolved vs. livestock) need not be different, as both involve multiple grazer species of different body size and potentially different diets (Bagchi & Ritchie 2010), and grazer-co-evolved plant species might persist under livestock grazing (Hart 2001). However, previous studies suggest that the two types of systems will be functionally dissimilar, that is have different effects on plant species composition, plant species pools, and the trajectory of plant community composition following release from grazing (Damhoureyeh & Hartnett 1997; Towne *et al.* 2005; Riginos & Young 2007). Functional dissimilarity might be due to several interrelated mechanisms. Firstly, the two groups differ in coevolutionary history with grazed plant species (McNaughton 1984, 1986), with indigenous herbivores having evolved with grassland plant species for up to millions of years (Frank *et al.* 1998), while domestic livestock systems are relatively young, having coexisted with grasslands for only the past 200 - 8000 years (McNaughton 1986; Bulliet *et al.* 2014), with many only in the past 200 years (McClaran & Anable 1992). One key outcome of these differing evolutionary histories is behavioral: wild, native grazers are free to migrate and adjust densities in response to changes in production (McNaughton 1986), while livestock grazing patterns are controlled by human managers. These different movement patterns could result in contrasting effects on plant species composition.

Secondly, domestic and native herbivores have been shown to exhibit differences in dietary selectivity (Peden *et al.* 1974; McNaughton 1978; Plumb & Dodd 1993; Augustine & McNaughton 1998; Burns *et al.* 2009; Bagchi & Ritchie 2010). Diet has been shown to affect plant community composition and diversity through shifts in the competitive balance of plant species and resultant effects on species colonization and extinction rates (Olff & Ritchie 1998; Frank 2005). Selection for, or preferential consumption (relative to its availability) of particular species or functional groups by all herbivore species (known as additive effects (Olff & Ritchie 1998; Ritchie & Olff 1999)), for example, could reduce competitive ability of dominant species and produce strong shifts in plant species composition. Previous studies have found differences across bison and cattle in their selectivity for certain plant functional types (Peden *et al.* 1974; Plumb & Dodd 1993) despite the two species' similar dietary digestive capacity. Other research has shown that, due to seasonal variation in levels of selectivity exhibited by native ungulates, native ungulates show lower dietary overlap among species, and thus higher niche separation, than domestic ungulate species of similar body size (Schwartz & Ellis 1981). Greater differentiation among herbivore species could result in compensatory effects, or less selective impacts on particular plant species despite possibly heavy biomass removals, resulting in relatively little overall impact of herbivory on plant species relative abundances.

Body size and its variation within an herbivore community, reflected by the number of herbivore species of different size grazing within an area, affects dietary selectivity (Olff & Ritchie 1998; Rook *et al.* 2004). Consequently, differences in the size and make-up of the herbivore assemblage between natural and managed systems may be another mechanism through which the two systems could exhibit functional dissimilarity. Large, diverse assemblages such as those found in natural systems may exhibit a net compensatory effect (*i.e.* no change in species composition despite significant biomass removal) while a net additive effect (*i.e.* directional shift in species composition) (Ritchie & Olff 1999) is more likely to be seen in smaller assemblages with higher overlap in diet selectivity, such as may occur in domestic livestock systems (Bagchi & Ritchie 2010). In South Africa, despite similarities in other metrics of plant community structure, Burns *et al.* (2009) found a significant difference in plant community composition between sites with multiple herbivores and sites with one or no herbivores, suggesting that the loss of multiple species from large herbivore assemblages, as typically occurs when native herbivore communities are replaced by livestock, could still result in a significant shift in plant species composition.

In this study, I compared impacts of past grazing and recovery of plant communities following relaxation of grazing in the Serengeti ecosystem. In my study area, domestic grazers consist primarily of three species: cattle, sheep, and goats, while the protected natural areas are home to more than 20 native species ranging from large species such as wildebeest, zebra and buffalo to mid-sized species including topi, impala, Grant's gazelles and reedbuck to the smaller Thomson's gazelles, among others. I expected that grazing in a livestock system, with its lower species diversity and higher overlap in diet selectivity (Bagchi & Ritchie 2010), would be more likely to have an additive effect and thus relaxing grazing would be more apt to produce a directional shift in plant species composition than in the more species-rich natural system. With a cumulative effect of grazing that is potentially compensatory, wildlife herbivores were expected to show little to no change in composition following a relaxation of grazing.

Following these expectations, this study tests the hypothesis that (1) past grazing has led to very different plant communities, and (2) relaxation of grazing in native and domestic systems will cause plant composition of the two systems to diverge, or to become more different from each other than initially, potentially exhibiting trajectories to different community states, defined by Schacht (1993) as distinct yet relatively stable plant communities that represent alternate 'climax' communities (Schacht 1993; van de Koppel *et al.* 1997; Bestelmeyer *et al.* 2003; Stringham *et al.* 2003).

These hypotheses were tested using an exclosure experiment at four pairs of sites within the Greater Serengeti Ecosystem (GSE), with each site pair consisting of a livestock-grazed site and a wildlife-grazed site that were environmentally and edaphically similar and located in close proximity. The effect of grazing intensity was measured at each site by creating plots with varying degrees of grazer exclusion through fencing and comparing these to reference plots where the current grazing regime was maintained. These plots were replicated across paired sites within two regions of the GSE. Initial and final wet-season species composition was measured for each plot and the Bray-Curtis dissimilarity across plots of paired management measured for each time point. Convergence or divergence in composition across the two management types was determined by the difference in dissimilarity between the two time points (*i.e.* whether composition of plots became more similar or more different).

As divergence in composition may depend upon the level of grazing pressure imposed (van de Koppel *et al.* 1997; van de Koppel & Rietkerk 2000), this study also tested the effect of average annual grazing intensity on these same compositional changes over time. Differences in grazing intensity have previously been shown to influence the effect of grazing on plant species composition (Milchunas *et al.* 1988; Hickman *et al.* 2004), likely in part due to the effect of grazing intensity on selectivity. Increasing grazing intensity is expected to decrease individual animal selectivity by changing total forage abundance and reducing available preferred forage per capita (Augustine & McNaughton 1998). Reducing selectivity could then affect composition through either positive effects on diversity (by preventing reduction or extinction of some species) or negative effects (through the loss of grazer control on competitive dominants).

I expected that decreasing grazing intensity (or increased protection from grazing) would be associated with a greater shift in species composition and greater magnitude of divergence in composition across management types. These hypotheses were tested by analyzing the effect of plot grazing intensity on 1) individual plot compositional change over time and 2) the change in paired plot dissimilarity over time.

METHODS

Study Site

The Greater Serengeti Ecosystem covers an area of over 30,000 km^2 (Melamari 2000) and is located along the Kenya-Tanzania border in northwestern Tanzania, East Africa (Figure 1). The ecosystem, defined by the movements of migratory wildebeest (*Connochaetes taurinus albojubatus*) herds, is comprised of a suite of protected areas: primarily Serengeti National Park (SNP) (14,763 km^2) and including, among others, Grumeti (420 km^2) and Kijereshi Game Reserves (GR), which lie to the south and west of SNP (Thirgood 2008). This study was focused along the western corridor of SNP (Figure 1), in areas along the borders of SNP and Grumeti Game Reserve (GGR) where large patches of open C_4 grassland dominate. These grasslands, together with the wide variety of other vegetation types across the park, allow the Serengeti to support over 30 species of ungulates numbering close to 2.5 million individuals (Maddock 1979). The migratory wildebeest (~1.3 million), zebra (*Equus quagga burchellii*) (~200,000), and Thomson's gazelle (*Eudorcas thomsonii*) (~440,000) form the majority (Sinclair *et al.* 2008).

Outside the protected areas of the GSE are open areas inhabited by various ethnic communities practicing agriculture, pastoralism, or more typically, some combination of the two (*i.e.* agropastoralism). Livestock species kept in these areas are primarily cattle, as well as smaller mixed herds of sheep and goats. The sites within the study area designated as protected, wildlife-dominated sites lie within either SNP or GGR and are paired with livestock-dominated sites located in adjacent open communal grazing areas (Figure 1). Mean annual precipitation at the study sites ranges from 750 – 1,000 mm/year (Sinclair *et al.* 2008) and soils are primarily sandy clay loams.

Measuring and Comparing Grazing Impacts

Two regions where impacts on plant species composition could be compared between a wildlife-dominated area and a livestock-dominated area were identified: (1) Kijereshi (KIJ): along the southwestern boundary of SNP and (2) Nata/Isenye (NAT): along the northern border of GGR (Figure 1). Both regions feature open areas with a mix of livestock grazing and small-scale agriculture that possess similar site characteristics to adjacent protected areas in either SNP or GGR (Table 1). In order to best compare the effect of management (*i.e.* whether area is grazed by livestock or wildlife), I established paired sites (one grazed predominantly by wildlife and one primarily by livestock) based on similarities in characteristics including vegetation type, mean annual rainfall, soil fertility and texture, and distance from drainages, as these factors have been shown to influence ecosystem properties (Yimer *et al.* 2006) (Table 1). I selected two sets of paired sites in each of the two regions for a total of 8 individual sites comprised of 4 management pairs (Figure 1). Site pairs were selected randomly from within comparable areas identified inside and outside of the protected areas.

Rainfall was measured locally at three locations in the study area: 1) Ndabaka gate, SNP – which provided the best available rainfall estimate for all sites in Kijereshi region (KIJ1, NP1, KIJ2, NP2); 2) Gambaranyera Hill, just outside GGR near Iharara village – which provided the estimate for ISE and GGR1; and 3) Sasakwa Hill, just outside GGR near Makundusi village – which provided the estimate for NAT and GGR2 sites.

Study Design

Once paired experimental sites were selected, twelve plots, representing four different fencing treatments replicated three times each, were established at each site. Plots were laid out in a grid fashion with 7 m between plots of different fencing treatments and 20 m separating each replicate. The short-term 1.5 x 1.5 m grazing exclosures were constructed using local, abundant thorn trees (*Dichrostachys cinerea*) (which, due to their relatively low economic value, were less likely to be removed from the site) and replenished as needed in order to maintain exclosure height. The four fencing treatments, intended to impose graduated levels of grazing intensity (GI), were created using a monthly fencing schedule to limit herbivore access to plots for various amounts of time throughout the year. Reference plots were maintained under 'normal' grazing conditions and left unfenced 100% of the time. Two intermediate fencing treatments were under a repeating three month schedule, during which plots would either be open to grazers for two months and then fenced for one (33% fenced) or fenced for two months and then unfenced for one (66% fenced). Finally, one plot in each replicate was imposed with a 100% fencing treatment in which fences were maintained at or near 100% of the time. These fencing schedules were adhered to as closely as possible, although occasionally a fence was found to be removed and was then replaced. This variability is accounted for in the calculation of plot grazing intensity, explained below. Treatments were initiated and fences erected in July 2010 and the experiment carried out through April 2011. While this fencing schedule was intended to incorporate seasonal variation throughout the year, it fails to account for grazing pulses that may happen at particular times of the year. However, as these pulses tend to occur primarily in wildlife-grazed areas (whereas livestock-grazed plots were observed to be grazed continuously throughout the year), this was taken to be one aspect of the difference in management.

Measurements

To classify soil texture and to measure concentrations of soil nutrients, five 10 cm deep (8 cm diam.) soil cores were randomly taken within the northeast, southeast, southwest, northwest and center locations of each site. Samples were air-dried, weighed, and then passed through a 2-mm sieve to separate the fine earth fraction. Clods not passing through the sample were crushed and passed through again, excluding gravel and rock fragments, etc. Soil texture was determined by determining the fractions of sand, silt, and clay present in each sample through mechanical particle size analysis. Samples were then analyzed for total nitrogen, (N) using the standard Kjeldahl Nitrogen method (Van Reeuwijk 1993) and for concentration of the plant nutrient phosphorous (P) with the Bray-1 extractable method (Bray & Kurtz 1945). The exchangeable base sodium (Na) was extracted using the ammonium acetate extraction method followed by analysis by AAS flame spectrophotometer (Van Reeuwijk 2006). Samples were also analyzed for percent organic carbon using the Walkley-Black procedure (Walkley & Black 1934). All soil analyses were conducted at Sokoine University of Agriculture, Tanzania. These data were used to aid in paired site selection.

To determine animal abundances and estimate densities of both livestock and wildlife in the study areas, transects ranging 7-27 km in length (depending on whether they encompassed 1 or 2 sites) were driven along vehicle tracks 2-3 times a month for 19 months. Transects were driven at varying times of day throughout each month to capture temporal variation in grazing patterns. Throughout transects, all large animal species spotted within 200 m of either side of the track were identified and counted. This spotting distance was chosen so as to avoid the bias of disproportionately counting larger, more visible species at farther distances. Animal counts were then converted to tropical livestock units based on average body weights for each species (FAO 1999) and these figures were used in calculating density.

To track monthly consumption of biomass as an estimate of a site's baseline grazing intensity, aboveground net primary production (ANPP) was measured using 1 m^2 movable exclosures at bi-monthly intervals to account for measureable changes in production (as in McNaughton 1979; McNaughton *et al.* 1996). All live plant biomass was clipped, dried, and weighed following McNaughton *et al.* (1996). Based on these measurements, grazing intensity for each interval was calculated as forage consumption relative to production:

$$\left(1-\left(\frac{Standing\ Biomass_{grazed}}{Standing\ Biomass_{ungrazed}}\right)*100\right) \tag{1}$$

(McNaughton 1985). The mean grazing intensity for the study duration was then calculated for each site.

Plant species composition was measured by identification of each species present in a plot and visual estimation of each species percent cover. Compositional surveys were completed at four different time points: 1) initially, when plots were set up, in the dry season of July 2010, 2) towards the end of the first wet season in April 2011, 3) during the second dry season in July 2011 and finally, 4) near the end of the second wet season in April 2012. All individual species were estimated except in a few cases (n = 3) where a plant could not always be identified down to species level and so these were lumped together by genus, or in the case of sedges, by functional group. Species richness (S) was calculated at each time point as the total number of species in a plot. Species diversity was measured using the Shannon-Wiener Index (H), equal to:

$$H = -\sum_{i=1}^{S} p_i * \ln(p_i) \tag{2}$$

where p_i is the proportional abundance of the i^{th} plant species in a plot. Lastly, community evenness (E), which compares similarity in abundance of each species present in a plot and ranges between 0 and 1, with 1 being equal proportional abundance across species, was calculated using the equation:

$$E = H/\ln(S) \tag{3}$$

These indices were compared across management type both at the final time point (wet season 2012) and as the shift across wet seasons (Wet_{2012} – Wet_{2011}) using t-tests in Microsoft Office Excel (2007).

Prior to analyzing compositional changes, a plot x species matrix for each region was built in Microsoft Office Excel (2007) for plot composition in wet seasons 1 and 2 and each species' percent frequency of occurrence across all plots examined. All species with <5% frequency of occurrence within all plots were then removed from the matrix, leaving only the more common species (N = 26 for KIJ; N = 29 for NAT) which together made up 96.11% and 98.65% of total plant cover for Kijereshi and Nata/Isenye regions, respectively (McCune & Grace 2002). Differences in wet-season plot community composition were measured using the Bray-Curtis dissimilarity index (BC), calculated as:

$$B_{jk} = 100\left(\sum_{i=1}^{n} \frac{|y_{ij} - y_{ik}|}{(y_{ij} + y_{ik})}\right) \quad (4)$$

where y_{ij} is the cover of the i^{th} species in the j^{th} sample, and y_{ik} is the cover of the i^{th} species in the k^{th} sample, summed across all n species (as in Bagchi 2009). This measure of shared abundance relative to total abundance ranges from 0 to 1, where a value of 0 means the plots had identical composition (share all species in common) and a value of 1 means the two plots did not have any species in common. This index is appropriate as it is influenced more strongly by changes among abundant species and less affected by changes among rare species (Krebs 1989).

To determine overall compositional change, the BC dissimilarity between the composition of a plot in wet season 1 (April 2011) to the composition of that same plot in wet season 2 (April 2012) was measured (BC_T), with a value close to 0 indicating the plot underwent little change in species composition and larger values representing greater change in the plot's composition over time.

Analyses

Differences in the species pool across regions (Sites 1-4: Kijereshi region; Sites 5-8: Nata/Isenye region; Figure 1, Table 1) and a large difference in the mean plot compositional change over time prompted a separation of the data into two separate datasets by region. A permutational multivariate analysis of variance was then done on each dataset using the plot x species matrix for wet seasons 1 & 2 and the *adonis* function in the vegan package of the statistical program R (R Core Team 2014). This function allows one to directly assess the effect of independent variables on plot dissimilarity as it operates on the matrix itself. Thus, the regional plot x species matrix was used as the dependent variable and the Bray-Curtis index as the method used to calculate pairwise distances across plots. The effects of management type, plot grazing intensity, and their interaction on plot dissimilarity were then analyzed. Management type was defined as either "wildlife-grazed" or "livestock-grazed" depending on the dominant herbivores using the site and for whom the site was primarily managed. Plot grazing intensity, expressed as a percent, was an index of months a plot was available to grazers (as determined by the plot's imposed fencing schedule and adjusted for any months fences were found disturbed or removed) multiplied by the mean site grazing intensity, calculated as described above.

A second *adonis* analysis was then done for each region on the species matrix for wet season 2 only. Here the effects of management type, plot grazing intensity, their interaction, and initial wet season species richness were analyzed for their effects on final plot species composition.

Regression analyses were done to evaluate relationships between shifts in the percent relative abundance of different functional groups (*i.e.* grasses, forbs, and sedges) and plot grazing intensity for both livestock-grazed and wildlife-grazed plots for each region. Differences across management in shifts in percent relative abundance and species and functional group richness across wet seasons were also tested using t-tests. Both t-tests and regressions were conducted in Microsoft Office Excel (2007).

Lastly, in order to better understand which species were driving any observed differences in community composition, a set of core species within each region (Supplemental Information S1) was identified at the end of wet season 2 (April 2012) by determining the percentage of a species' presence in livestock-grazed and wildlife-grazed plots. A species was included in the regional set of core species (Supplemental Information S1) if it was present in $>20\%$ of all plots or $>25\%$ of all plots within one management type.

The difference in percent cover across wet seasons ($\Delta C = C_{2012} - C_{2011}$) of each of these core species were then used as dependent variables in a multivariate analysis of variance done in SPSS (IBM Corp. 2011) to determine the significance of management, plot grazing intensity, and an interaction between the two in explaining individual species' shifts across years.

RESULTS

Rainfall estimates were obtained only for the months October – April for the time periods of 2010-2011 (year 1) and 2011-2012 (year 2), as these are the months when most of the rain falls in these areas (Sinclair *et al.* 2008). Rainfall increased from year 1 to year 2 at all locations and was positively associated with the change in mean plot species richness from wet season 1 (April 2011) to wet season 2 (April 2012) among all plots at associated sites ($R^2 = 0.8536$) such that fewer species were lost on average in plots within areas that received a greater increase in rainfall.

The average herbivore density was 190.05 TLUs/km^2 (85.60 TLUs/km^2 in KIJ and 294.50 TLUs/km^2 in NAT) on transects within livestock-grazed areas and 92.16 TLUs/km^2 (123.43 TLUs /km^2 in KIJ and 60.90 TLUs /km^2 in NAT) on transects within wildlife-grazed areas. Livestock made up an average of 21.06% of TLUs on transects within wildlife-grazed areas (42.12% within GGR, 0% in SNP) and wildlife made up an average of 2.75% of herbivores on transects in livestock-grazed areas (5.12% in KIJ, 0.37% in NAT) (Bagchi & Ritchie 2010).

Estimated site-level grazing intensity over the study duration ranged from 40.40% to 74.84% with a mean across all sites of 61.66%. Plot-level grazing intensity (after accounting for proportion of time protected by fencing) ranged from 0% to 74.84% with a mean across all plots of 34.48%. There was no significant difference in either mean site (n = 8, $p = 0.24$) or plot (n = 96, $p = 0.06$) grazing intensity across management.

Past Grazing Impact: Differences in Initial Composition

The total number of species found within all plots in the Kijereshi region (n = 48) in the first wet season of April 2011 was 47 species. Dominant species at this time were the grasses *Chrysochloa orientalis* and *Sporobolus ioclados*. In the Nata/Isenye region, the total number of species within all plots (n = 48) was 44 species in the first wet season and dominant species were primarily the grasses *Chrysochloa orientalis*, *Themeda triandra*, and *Panicum coloratum*. Across both regions, livestock-grazed plots had lower mean species richness than wildlife-grazed plots in the initial wet season, though this difference was significant only for NAT region (n = 48, $p < 0.0001$) (Table 2). Despite lower overall species richness, livestock-grazed plots initially had higher mean grass species richness than wildlife-grazed plots, but this difference was significant only for KIJ region (n = 48, $p = 0.003$) (Table 2). Forb species richness was lower in all livestock-grazed plots, but not significantly so in either region.

In Kijereshi region, mean composition of livestock-grazed plots in the wet season of 2011 was comprised of 85.22% grass relative abundance, 4.48% forbs and 10.30% sedges compared to 67.14% grass, 23.27% forbs, and 9.58% sedge relative abundance in wildlife-grazed plots (Figure 2). In Nata/Isenye, livestock-grazed plots had 95.21% grass relative abundance, 2.09% forbs, and 5.40% sedges compared to 87.99% grass, 10.49% forbs, and 1.52% sedges in wildlife-grazed plots (Figure 2). Significant differences existed across management type in percent relative abundance of all functional groups in both regions, with the exception of sedges in KIJ region (Table 3).

Effects of Grazing Treatments on Final Composition

Following ~21 months of treatment, the wet season composition of all plots changed by an average Bray-Curtis dissimilarity (BC_T) of 0.276 ± 0.012, with site means ranging from 0.336 ± 0.012 – 0.421 ± 0.011 in KIJ region and 0.163 ± 0.005 – 0.175 ± 0.006 in NAT region. Plots in KIJ region (mean $BC_T = 0.382 \pm 0.008$) showed significantly greater compositional change across wet seasons than plots in NAT region (mean $BC_T = 0.169 \pm 0.003$, $p < 0.0001$).

Plot grazing intensity had a weak negative effect on the final (April 2012) Shannon diversity (n = 48, $R^2 = 0.077$, $p = 0.057$) and evenness (n = 48, $R^2 = 0.098$, $p = 0.030$) of plots within KIJ region. It also had a significant positive effect on the 2012 percent relative abundance of grasses (n = 48, $R^2 = 0.120$, $p = 0.016$) and a significant negative effect on the 2012 percent relative abundance of forbs across all KIJ plots (n = 48, $R^2 = 0.206$, $p = 0.001$) and a similar, albeit weaker, negative effect on forbs across NAT plots (n = 48, $R^2 = 0.099$, $p = 0.030$) (Figure 3). These trends were in a similar direction across both livestock-grazed and wildlife-grazed plots, but were stronger and statistically significant only for livestock-grazed plots in KIJ (grass: n = 24, $R^2 = 0.154$, $p = 0.058$; forb: n = 24, $R^2 = 0.237$, $p = 0.016$) and wildlife-grazed plots in NAT (forb: n = 24, $R^2 = 0.136$, $p = 0.051$).

The *adonis* analysis for KIJ region revealed significance of all variables in explaining dissimilarity across all plots from wet seasons 1 & 2 but particularly interesting was a significant interaction between management and plot grazing intensity (p = 0.024), suggesting that the grazing treatment affected livestock-grazed and wildlife-grazed plots differently. Specifically, these different effects were seen in the changing abundance of particular species. There were two species that showed significantly different shifts in percent cover across management: the grass, *Chrysochloa orientalis* (n= 48, $p = 0.014$) and the forb, *Indigofera hochstetteri* (n= 48, $p = 0.048$). In livestock-grazed plots, *C. orientalis* exhibited a decrease in cover of 3.2%, while in wildlife-grazed plots it increased by 0.7% (n = 48, $p = 0.001$). On the other hand, *I. hochstetteri* increased in percent cover in livestock-grazed plots by 7.7%, while it decreased by 0.3% in wildlife-grazed plots (n = 48, $p = 0.004$). Furthermore, the interaction between management and plot grazing intensity was significant in explaining the shift in percent cover for three forb species: *Justicia matamensis* ($p = 0.050$), *Portulaca* spp. ($p = 0.050$), and *Commelina* spp. ($p =$

0.048), and marginally significant in explaining the shift of one grass species: *Microchloa kunithii* ($p = 0.056$) in Kijereshi region. In the case of *J. matamensis* and *Portulaca* spp., plot grazing intensity had an effect only in wildlife-grazed plots and was non-significant in livestock-grazed plots. In wildlife-grazed plots, the percent cover of *J. matamensis* decreased (n = 48, $R^2 = 0.154$, $p = 0.058$) with increasing plot grazing intensity while percent cover of *Portulaca* spp. increased (n = 48, $R^2 = 0.191$, $p = 0.033$). Conversely, the shift in percent cover of *Commelina* spp. and *Microchloa kunithii* were affected by plot grazing intensity only in livestock-grazed plots, where it had a positive effect on *M. kunithii* (n = 48, $R^2 = 0.280$, $p = 0.008$) and a negative effect on *Commelina* spp. (n = 48, $R^2 = 0.238$, $p = 0.016$). Plot grazing intensity alone had no significant effects on the shift in percent cover of core species in Kijereshi region.

When considering only final plot composition, however, neither plot grazing intensity ($p = 0.083$) or the interaction between management and plot grazing intensity ($p = 0.088$) was significant in explaining dissimilarity across KIJ plots. Management still had a significant effect ($p = 0.005$), as did initial wet season species richness ($p = 0.001$). Species that had disappeared completely or fallen below < 5% frequency of occurrence in all plots from wet season 1 to wet season 2 included the grasses: *Sporobolus festivus*, *Digitaria macroblephara*, *Chloris pycnothrix*, *Chloris gayana*, and *Eragrostis exasperata*; the forbs: *Orthosiphon parvifolius*, *Crotalaria barkae*, *Chlorophytum bakeri*, *Euphorbia inaequilatera*, *Indigofera volkensii* and the shrub *Solanum dubium*.

In the *adonis* analysis for Nata/Isenye region, management ($p < 0.001$) was the only significant variable explaining dissimilarity across plots, indicating that for this short time period, the grazing treatments did not significantly affect compositional change (plot grazing intensity: $p = 0.943$). However, plot grazing intensity did still have a significant effect on the shift in percent cover of two individual grass species: *Chrysochloa orientalis* (n= 48, $p = 0.011$) and *Digitaria macroblephara* (n= 48, $p = 0.009$). The effect of grazing intensity was opposite for these two species, with grazing intensity increasing the percent cover of *Chrysochloa orientalis* (n= 48, $R^2 = 0.146$, $p = 0.007$) and decreasing it for *Digitaria macroblephara* (n= 48, $R^2 = 0.159$, $p = 0.005$). Surprisingly, management did not have a significant effect on the shift in percent cover of any core species in the region, indicating that the initial dissimilarity across management was conserved over time. This is also illustrated by the maintenance of significant differences in species richness and forb and sedge percent relative cover (Tables 2 & 3). Lastly, there was one grass, *Sporobolus pellucidus,* that showed a weak effect ($p = 0.061$) of the interaction between management and plot grazing intensity on its shift in percent cover, with grazing intensity reducing it in wildlife-grazed plots (n = 48, $R^2 = 0.107$, $p = 0.120$) and increasing it in livestock-grazed plots (n = 48, $R^2 = 0.096$, $p = 0.141$).

For final composition only, management ($p = 0.010$) was again the only significant variable in the *adonis* analysis explaining dissimilarity across all NAT plots. The remaining variables were highly nonsignificant (plot grazing intensity: $p = 0.675$, initial wet season species richness: $p = 0.867$, and the interaction between plot grazing intensity and management: $p = 0.355$). Species in this region that disappeared or were reduced below 5% frequency of occurrence across all plots included the grasses: *Digitaria ternata*, *Cynodon dactylon*, *Eragrostis tenuifolia*, *Pennisetum mezianum*, and *Setaria sphacelata*; the forbs: *Justicia matamensis*, *Sida cuneifolia*, and *Gutenbergia petersii*, and the shrub *Solanum incanum*. The forb *Cassia fallacina* and the shrub *Solanum dubium*, on the other hand, became more common in the second year, increasing from wet season 1 to wet season 2 to over 5% frequency of occurrence across plots.

Effects of Grazing Treatments on Compositional Similarity across Management

In KIJ region, livestock-grazed plots and wildlife-grazed plots exhibited similar shifts in the mean percent relative abundance of all three functional groups (Figure 4a). Yet interestingly, across both regions, livestock-grazed and wildlife-grazed plots differed in the magnitude of change in relative abundance that occurred for functional groups across time. While livestock-grazed plots in both regions showed significant decreases in grass mean percent relative abundance and an increase in forbs (KIJ, $p = 0.012$) and sedges (NAT, $p < 0.001$) (Table 4), wildlife-grazed plots in both regions stayed stable and showed no significant change in the mean percent relative abundance of any functional group over the duration of the experiment (Table 4). However, despite the replacement of grass cover by forb cover in KIJ region, livestock-grazed and wildlife-grazed plots maintained significant differences in mean percent relative abundance in both of these functional groups across years (Table 3, Figure 2). In NAT region, livestock-grazed and wildlife-grazed plots differed in the mean shift in percent relative abundance of both grasses ($p = 0.001$) and sedges ($p < 0.001$) (Figure 4b). The reduction in grass mean percent relative abundance in livestock-grazed plots and slight gain in wildlife-grazed plots eliminated any significant difference of this functional group across management but the greater increase in sedge abundance in livestock-grazed plots only served to widen the gap in similarity of this functional group across livestock-grazed and wildlife-grazed plots (Table 3, Figure 2).

Change in plot species richness from 2011 to 2012 was also significantly different across management, with wildlife-grazed plots in KIJ showing a larger loss in forb species richness ($p = 0.046$) across years than livestock-grazed plots (Figure 5a). Despite these greater shifts, there was still no significant difference in forb richness or total species richness across management in 2012 (Table 2). Further, there was no significant difference in the loss of grass species richness across years in KIJ, which served to maintain the initial difference across management (Table 2). In NAT plots, livestock-grazed plots lost significantly more grass species across years ($p = 0.037$, Figure 5b), yet this difference was not enough to cause mean grass species richness in 2012 to differ across management (Table 2). On the contrary, wildlife-grazed plots lost significantly more total species than did livestock-grazed plots ($p = 0.003$, Figure 5b) and the mean difference across the two systems was maintained (Table 2). Forb species richness did not change in significantly different ways and remained similar in 2012 (Table 2).

DISCUSSION

Functional similarity between livestock grazers and native wildlife grazers was determined by analyzing differences in initial plant species composition across management and by tracking changes in composition through time following relaxation of grazing. Figure 6 below offers a framework illustrating hypothetical initial composition across management types and possible pathways of compositional change and details the implications of each scenario. Different initial composition across management (Figure 2, Table 3) could suggest functional dissimilarity across the two types of grazing systems (Figure 6). A reduction in this difference over time reflects convergence in composition (outcome 1, Figure 6) and suggests *resiliency* of the plant community despite differing effects of grazing. On the other hand, a difference in final composition that is greater than or equal to initial differences suggests that grazing by the two groups has set communities on alternate pathways (Schacht 1993; van de Koppel *et al.* 1997; Stringham *et al.* 2003). This result reflects either further divergence in composition (final difference > initial; Outcome 2, Figure 6) or simply through a maintenance of differences (final difference = initial; Outcome 3, Figure 6).

This study tested for the effects of management (dominant grazer type) and grazing intensity through a replicated set of paired livestock-grazed and wildlife-grazed sites with similar edaphic and environmental characteristics. While there did exist significant initial differences in some measures of composition across management type (hypothesis 1), the initial short-term community trajectories are not consistent with the hypothesis of divergence in composition following a reduction in grazing (hypothesis 2; outcome 2, Figure 6). However, it should be noted that the effect of plot grazing intensity was only significant in one region (KIJ), which suggests that compositional change in NAT region, at least, is likely more a reflection of temporal variation in resources than an effect due to relaxed grazing. Due to this and to the limited duration of the experiment, it is not possible to draw conclusions about longer term community paths, such as whether grazer exclusion causes communities to reach alternate ‘states’ of community composition. However, this study does provide evidence that management type is significant in explaining differences in plant community composition across livestock-grazed and wildlife-grazed areas despite controlling for differences in plot grazing intensity and that these differences, reflected in plot species richness (Table 2) and functional type abundance (Table 3, Figure 2), persist across management type over at least two wet seasons.

Past Grazing Impact: Differences in Initial Composition

Initially, wildlife-grazed plots had, on average, more species ($p < 0.0001$ for NAT, Table 2) and greater forb cover ($p < 0.0001$ for both regions, Table 3) than livestock-grazed plots although livestock-grazed plots had a greater number of grass species ($p < 0.0001$ for KIJ, Table 2) and higher grass cover ($p < 0.0001$ for KIJ, $p = 0.011$ for NAT, Table 3). This result supports, to some extent, hypothesis 1: that past grazing has caused some initial differences in plant community composition. This result also partially contradicts an earlier finding by Bagchi & Ritchie (2010) that sites in the Trans-Himalayas grazed by native herbivores had higher initial forb *and* higher initial grass biomass than sites grazed by domestic livestock.

Effects of Grazing Treatments on Compositional Changes over Time

Plot species richness declined, on average, across all plots and resulted in more similar mean richness across livestock-grazed and wildlife-grazed plots (Table 3). This decline was likely a primary driver in individual plot compositional shifts over time (BC_T), with most plots losing rare and uncommon plant species, as the dominant species’ within each study region remained the same and plots experienced almost no change in mean Shannon diversity or evenness. Exclusion of grazing (at any level) led to relatively little change in species or functional group richness by year 2, as expected for the higher mean annual rainfall conditions of the study sites (Anderson *et al.* 2007), though it did have weak negative effects on 2012 forb species richness and 2012 plot evenness.

Plot grazing intensity was negatively associated with plot compositional change in Kijereshi region but had no effect in Nata/Isenye. The significantly greater mean change in plot composition across wet seasons in Kijereshi (mean $BC_T = 0.382 \pm 0.008$) than in Nata/Isenye (mean $BC_T = 0.169 \pm 0.003$, $p < 0.0001$) may have contributed to this. Plots in Nata/Isenye may have been more resistant to overall compositional change or slower to respond to changes in grazing intensity due to the region's more intense grazing history. A stronger history of intense grazing may have resulted in stronger selection for grazing tolerant species that are less likely to respond to a relaxation in grazing.

Furthermore, the lower rainfall of the first year of the study was below average (Sinclair *et al.* 2008) and is believed to have caused the loss of some species, primarily grasses and forbs, in the second year. Precipitation increased at all sites over the course of the study and while this was associated with a decrease in mean species richness across all plots, this effect was smaller for those with the biggest increase in annual rainfall. This is generally consistent with Adler and Levine's (2007) findings that species richness is influenced by previous-year precipitation and that higher richness results with greater increases in precipitation (Adler & Levine 2007). Thus, had species richness been measured an additional year, an increase in species richness (following the greater rainfall in year 2 of the study) would have been expected. Nonetheless, the lower overall richness observed across all plots in year 2 may have contributed to smaller compositional differences across plots.

Despite the fact that the Serengeti is a highly productive and dynamic system, the short duration of fencing protection may not have been adequate enough to produce greater dissimilarity between fenced and unfenced plots. Anderson *et al.* (2007) studied compositional similarity after six years of grazer exclusion in the Serengeti and still found only a weak, nonsignificant difference across plots within a site.

In both regions (with the exception of forbs in NAT), shifts in functional group mean percent relative abundance were larger in managed livestock-grazed areas than in natural wildlife-grazed areas. This result is similar to Bagchi & Ritchie's (2010) finding in a comparable experiment in the Indian Himalayas and implies that compositional change following exclusion or relaxation of grazing is faster in livestock systems than in wild grazer systems. Bagchi & Ritchie (2010) found that the larger shift in composition in livestock areas was driven by a large increase in forb relative abundance at the expense of sedges. This recovery of forbs in ungrazed livestock-managed areas, which the authors found to be due to the livestock species' strong preference for and selectivity of forbs, increased similarity of fenced plots in the livestock managed areas to those in natural wildlife areas. Anderson *et al.* (2007) also found that compositional similarity between grazed and ungrazed plots at higher rainfall sites in Serengeti was due to increased forb richness within exclosures and greater sedge richness in grazed plots, likely a result of selective grazing that reduced preferred plants such as forbs and thus increased more grazing-tolerant plants such as sedges and grasses. The decrease I observed in forb percent relative abundance across years with increasing grazing intensity supports the idea that such a preference exists in these areas as well and that protection from grazing allowed a possible release from grazer selectivity for forbs. This trend was similar across management types.

Effects of Grazing Treatments on Compositional Changes across Management Type

Between years, livestock-grazed plots lost more grass species, fewer forb species (KIJ), and overall fewer total species than did wildlife-grazed plots (Table 2), which helps explain the general increase in similarity over time between livestock- and wildlife-grazed plots. Livestock- and wildlife-grazed plots had the same or more similar mean species, grass, and forb richness in the second wet season than in the first (Table 2), suggesting that at similar levels of grazing intensity, functional similarity is increased (outcome 1, Figure 6), highlighting the resiliency of livestock-grazed plant communities. While wildlife-grazed plots showed no significant change in percent relative abundance across seasons, livestock-grazed plots experienced increases in forb (KIJ) and sedge (NAT) percent relative abundance in place of grasses (Table 4), another mechanism which served to increased similarity of plots across management (Figure 2). These results are consistent with Anderson *et al.*'s (2007) finding that at higher rainfall sites in the Serengeti, removal of herbivores leads to relatively little change in species richness, but can cause dramatic turnover of plant species and functional groups. One interesting difference between community responses across the two regions, however, is that each functional group shifted in the *same* direction within both livestock-grazed and wildlife-grazed plots in

Kijereshi region (Figure 4a), while in Nata/Isenye region, grass percent relative abundance shifted in *opposite* directions across management (Figure 4b). These consistent shifts in Kijereshi region, which led to significant changes over time in livestock-grazed plots but not in wildlife-grazed plots (Table 4), allowed livestock-grazed plots to begin to “catch up” to percentages found in wildlife-grazed plots (Figure 2). In Nata/Isenye region, because the magnitude of shifts of grasses and sedges were significantly larger in livestock-grazed plots than in wildlife-grazed plots (Figure 4b) and, as in KIJ region, the changes in wildlife-grazed plots were not significant over time (Table 4), livestock-grazed plots here too had a chance to “catch up”, if only in more similar grass percent relative abundance, which represents the majority of plot vegetation cover (Figure 2). Similar trends in functional type abundance could indicate greater functional similarity across the two types of grazing systems when under comparable levels of grazing (outcome 1, Figure 6).

While it is possible that the duration of the study was too limited to detect a divergent effect, under typical grazing conditions and at similar levels of protection, composition of plots in livestock- and wildlife-grazed areas did at least begin to converge (outcome 1, Figure 6), a result which contradicts the expectation of hypothesis 2. The overall increase in similarity across all plots under grazing could be due to the dominance in abundance of a relatively small group of grazing tolerant species (primarily grasses) (McNaughton 1985) that express despite drier conditions. *Chrysochloa orientalis*, *Sporobolus ioclados*, and *Themeda triandra* were the three most dominant species in both livestock-grazed and wildlife-grazed plots in both regions across years and all three species became more similar across management in their percent relative abundance from April

2011 to April 2012. These three grass species together initially made up 70.54% and 62.55% (a difference of 7.99%) of total plant percent relative abundance in livestock-grazed and wildlife-grazed plots across both regions, respectively, and 60.82% and 56.75% (a difference of 4.07%) of the totals in 2012.

Whether the exclusion of herbivores may eventually lead to a shift to a different stable state may ultimately depend more on the timing and spatial distribution of grazing as dictated by freedom of animal movement (McNaughton 1984, 1986) than on herbivore species composition, cumulative dietary preferences or other mechanisms (Westoby 1985). This is due to the fact that in situations in which herbivore density is dependent on vegetation conditions (as in most natural, wildlife-grazed systems), herbivore numbers should decrease (through starvation) once the standing crop falls below a certain threshold (van de Koppel *et al.* 1997; van de Koppel & Rietkerk 2000). In the Serengeti and other natural systems, wildlife herbivores tend not to reduce standing crop below that threshold due to migratory behavior that allows plant recovery and growth. On the other hand, in any system where management aims to maintain animal numbers (Illius & O'Connor 1999), such as is the case in livestock-grazed systems, herbivore density will increase independent of vegetation conditions (uncoupled to plant growth) (van de Koppel *et al.* 1997). This independence of herbivores from vegetation conditions is exacerbated by increasing settlement of herders around villages, farms and artificial water points, as well as improvements in protection from predators and disease (Skarpe 1991; van de Koppel *et al.* 1997). The continuous grazing pressure on one area of the landscape that results from the uncoupling of herbivores from vegetation conditions is the primary basis for the hypothesis that livestock systems may cause irreversible changes in plant communities, while natural systems grazed by wild herbivores are far less likely to do so (van de Koppel & Rietkerk 2000). Nonetheless, the similarity in composition across management types observed in this study under the current grazing regime suggests that livestock have not yet moved into a transition or pathway towards an alternate "overgrazed" state that might persist even in the absence of grazing (van de Koppel *et al.* 1997).

BROADER IMPLICATIONS

As the direction of a community transition depends on rainfall and soil conditions at a site, with greatest effects generally occurring in lower rainfall sites and clay soils (as a result of soil moisture availability) (Illius & O'Connor 1999; Anderson *et al.* 2007), it would be useful to test these hypotheses across a broader range of soil and rainfall conditions. This suggests that pastoral systems in more arid environments are more likely to see rapid changes in composition following grazer exclusion and, potentially, more prone to experience an irreversible state change under prolonged, intense grazing. Furthermore, while sites in and around the GSE are currently less prone to great shifts in composition from sustained, heavy grazing pressure, the increasing unpredictability in the magnitude and timing of rainfall due to the rapidly changing climate may bring an increased risk of adverse grazer impacts to more productive systems.

CONCLUSIONS

Effects on species composition due to grazing, unlike rainfall, may be relatively small on an annual scale but are often cumulative and significant over the long term, as the direction of the effect tends to be consistent for a given set of herbivore species (Illius & O'Connor 1999). In the Greater Serengeti Ecosystem of Tanzania, this study found that even over the span of two wet seasons, grazing by both livestock and native herbivores can have measurable effects on the percent relative abundance of different functional groups, with grasses positively associated with grazing intensity and forbs negatively related.

Furthermore, this study showed that despite initial differences, livestock-grazed and wildlife-grazed systems exhibit slight convergence of plant species composition when managed at similar levels of annual grazing intensity. These results suggest that, at least in a relatively productive grassland system, livestock and wildlife herbivores may be more functionally similar than previously suspected and that observed compositional differences across management type may be more attributable to aspects of management (annual grazing pressure, animal movement, and spatial and temporal patterns of grazing) (Ellis & Swift 1988; Illius & O'Connor 1999) than to functional differences in herbivore type or variation in cumulative effects of differing herbivore assemblages.

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Table 1. Environmental characteristics of paired study sites in the GSE.

Site Pair*	Site	Region	Mgmt°	MAR (mm) §	Total exchangeable bases (cMolc/kg)€	Soil Texture	Vegetation Category	Distance to nearest drainage (m)
1	KIJ1	Kijereshi	LS	750-850	20-25	Sandy clay loam	Open grassland	1000
1	NP1	Kijereshi	WL	750-850	20-25	Sandy clay loam	Open grassland	1000
2	KIJ2	Kijereshi	LS	750-850	20-25	Sandy clay/clay loam	Open grassland	2000
2	NP2	Kijereshi	WL	750-850	20-25	Sandy clay loam	Open grassland	2000
3	ISE	Nata	LS	>1000	15-20	Clay loam	Mixed *Acacia* woodland/ grassland	300
3	GGR1	Nata	WL	>1000	15-20	Clay	Mixed *Acacia* woodland/ grassland	300
4	NAT	Nata	LS	>1000	15-20	Sandy clay loam	Mixed *Acacia* woodland/ grassland	300
4	GGR2	Nata	WL	>1000	15-20	Sandy clay loam	Mixed *Acacia* woodland/ grassland	350

* Site pairs represent paired livestock-grazed and wildlife-grazed sites with similar environmental characteristics. The study included 8 sites, made up of 4 site pairs, 2 from each of two regions.

° Mgmt = Management and refers to whether the site was predominantly livestock-grazed (LS) or wildlife-grazed (WL).

§ Rainfall data: TANAPA, unpub. Data 2012 & VIP Singita, unpub. Data 2012

€ Total exchangeable bases, a proxy for soil fertility, is calculated from total cation exchange capacity and % base saturation (sum of Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}); Sinclair *et al.* 2008

Table 2. Differences by year in mean plot richness of species and functional groups across management type.

Kijereshi Region

2011	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	4.50 ± 0.51	2.63 ± 0.28	1.87	**0.003**
Forbs	2.88 ± 0.40	3.92 ± 0.39	-1.04	0.067
Overall Species	8.88 ± 0.75	10.13 ± 0.49	-1.25	0.172

2012	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	3.54 ± 0.25	2.42 ± 0.19	1.12	**< 0.001**
Forbs	2.67 ± 0.22	2.42 ± 0.22	0.25	0.425
Overall Species	7.83 ± 0.22	7.71 ± 0.28	0.12	0.793

Nata/Isenye Region

2011	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	6.13 ± 0.32	5.63 ± 0.39	0.50	0.333
Forbs	2.50 ± 0.35	2.83 ± 0.31	-0.33	0.477
Overall Species	7.92 ± 0.41	11.63 ± 0.61	-3.71	**< 0.0001**

2012	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	4.58 ± 0.25	5.25 ± 0.25	-0.67	0.064
Forbs	1.88 ± 0.19	2.54 ± 0.28	-0.66	0.054
Overall Species	7.58 ± 0.32	9.17 ± 0.38	-1.59	**0.003**

Table 3. Differences by year in the percent mean relative abundance of functional groups across management type.

Kijereshi Region

2011	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	85.22	67.14	18.08	< 0.0001
Forbs	4.48	23.27	-18.79	< 0.0001
Sedges	10.30	9.58	0.72	0.760

2012	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	71.99	59.67	12.32	0.028
Forbs	12.06	27.69	-15.63	< 0.001
Sedges	15.95	12.64	3.31	0.383

Nata/Isenye Region

2011	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	92.51	87.99	4.52	0.011
Forbs	2.09	10.49	-8.39	< 0.0001
Sedges	5.40	1.52	3.87	< 0.0001

2012	LS-grazed	WL-grazed	Δ LS-WL	*p*
Grasses	87.88	88.95	-1.07	0.586
Forbs	1.63	8.50	-6.87	< 0.001
Sedges	10.49	2.56	7.93	< 0.0001

Table 4. Shifts in the percent mean relative abundance of functional groups across wet seasons within livestock-grazed and wildlife-grazed plots.

Kijereshi Region

Livestock-grazed	**2011**	**2012**	**Δ 2012-2011**	***p***
Grasses	85.22	71.99	-13.23	**0.002**
Forbs	4.48	12.06	7.58	**0.012**
Sedges	10.30	15.95	5.65	0.070

Wildlife-grazed	**2011**	**2012**	**Δ 2012-2011**	***p***
Grasses	67.14	59.67	-7.47	0.153
Forbs	23.27	27.69	4.42	0.286
Sedges	9.58	12.64	3.06	0.350

Nata/Isenye Region

Livestock-grazed	**2011**	**2012**	**Δ 2012-2011**	***p***
Grasses	92.51	87.88	-4.63	**0.003**
Forbs	2.09	1.63	-0.46	0.471
Sedges	5.40	10.49	5.09	**<0.001**

Wildlife-grazed	**2011**	**2012**	**Δ 2012-2011**	***p***
Grasses	87.99	88.95	0.96	0.652
Forbs	10.49	8.50	-1.99	0.362
Sedges	1.52	2.56	1.04	0.117

FIGURE CAPTIONS

Figure 1. Greater Serengeti Ecosystem with study regions 1) Kijereshi and 2) Nata/Isenye shown in inset and site locations marked.

Figure 2. Initial (April 2011) and final (April 2012) wet season species composition of livestock-grazed and wildlife-grazed plots expressed as mean percent relative abundance of grasses, forbs, and sedges for both regions. In Kijereshi region, both groups show increases in forb and sedge percent relative abundance at the expense of grasses. In Nata/Isenye region, percent relative abundance of grasses stayed relatively stable.

Figure 3. Significant effect of plot grazing intensity on the final (April 2012) percent relative abundance of grasses ($R^2 = 0.120$, $p = 0.016$) and forbs ($R^2 = 0.206$, $p = 0.001$) across all KIJ plots (n = 48) and of forbs ($R^2 = 0.099$, $p = 0.030$) across all NAT plots (n = 48). There was no significant effect of plot grazing intensity on final percent relative abundance of grasses in NAT or of sedges in either region.

Figure 4a. For Kijereshi region, the mean shift in percent relative abundance of functional groups across wet seasons did not significantly differ by management type.

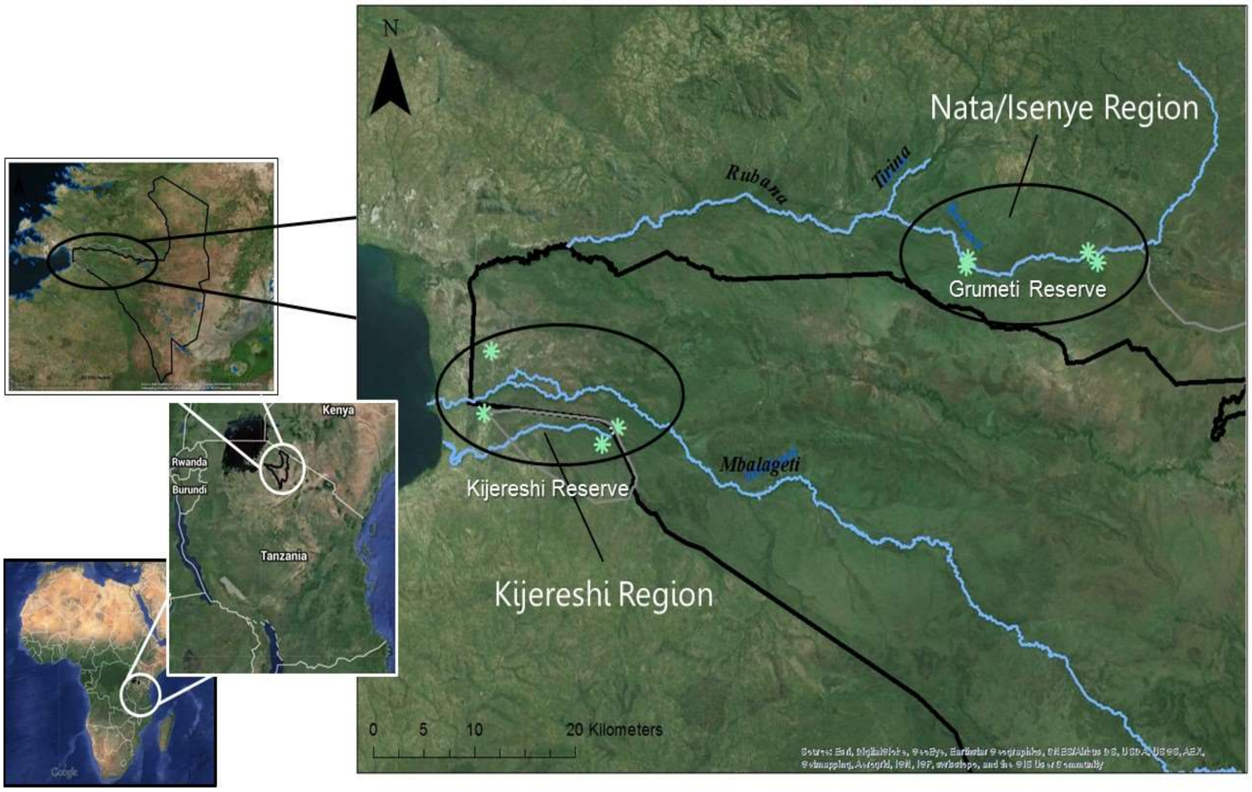
Figure 4b. For Nata/Isenye region, livstock-grazed plots and wildlife-grazed plots exhibited significantly different mean shifts in percent relative abundance of grasses ($p = 0.001$) and sedges ($p < 0.001$) across wet seasons.

Figure 5a. Mean change in plot forb species richness from wet season 1 (April 2011) to wet season 2 (April 2012) was significantly different in livestock- and wildlife-grazed plots in Kijereshi region ($p = 0.046$). Negative numbers indicate a loss in species richness over time.

Figure 5b. In Nata/Isenye region, the mean change in plot species richness from wet season 1 (April 2011) to wet season 2 (April 2012) was significantly different in livestock- and wildlife-grazed plots for grass species ($p = 0.037$) and for total species richness ($p = 0.003$). Negative numbers indicate a loss in species richness over time.

Figure 6. Conceptual framework illustrating hypothetical composition of livestock- and wildlife-grazed plots and possible pathways of compositional change following relaxation of grazing. The framework assumes livestock-grazed and wildlife-grazed plots begin with different composition and shows how composition of plots may become more similar (converge) or stay or become more different (diverge).

Figure 1.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2.

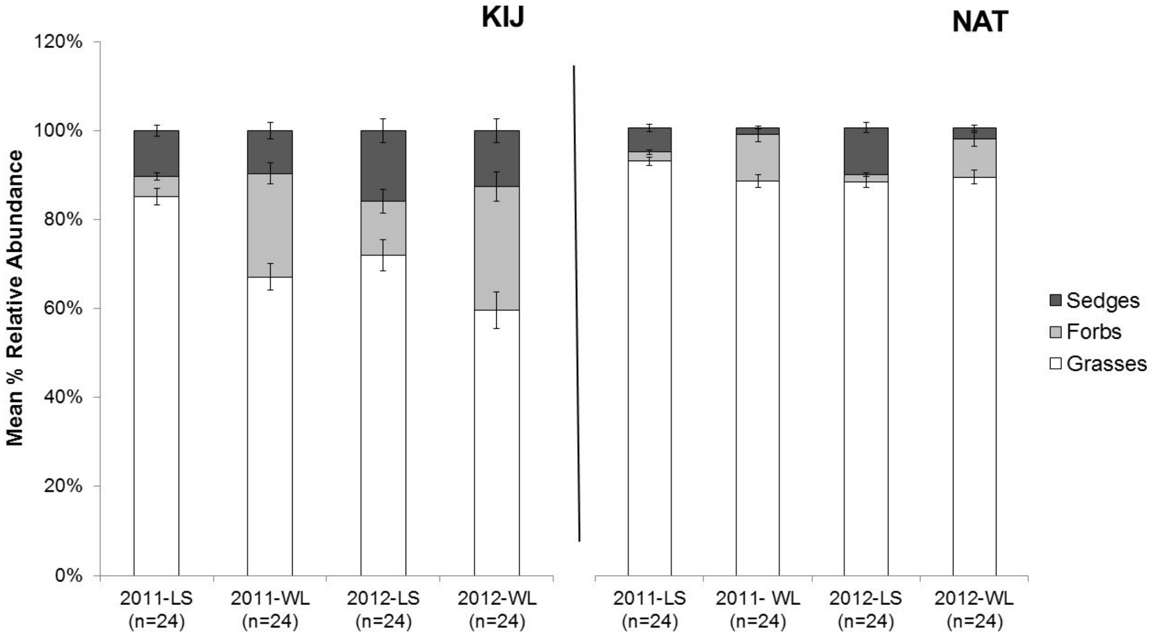


Figure 3.

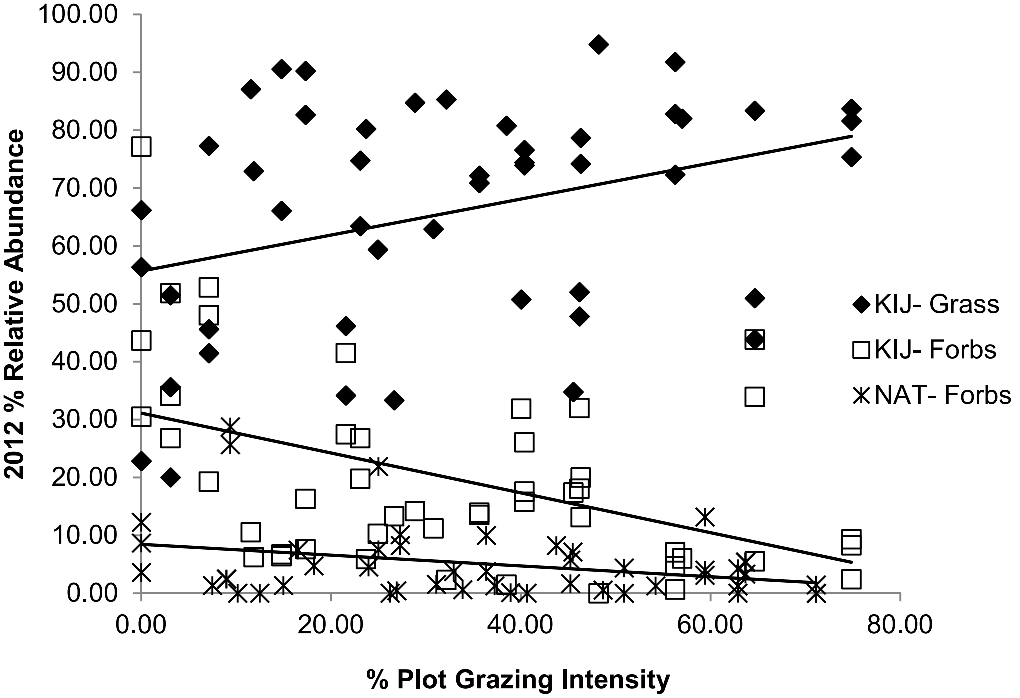


Figure 4a.

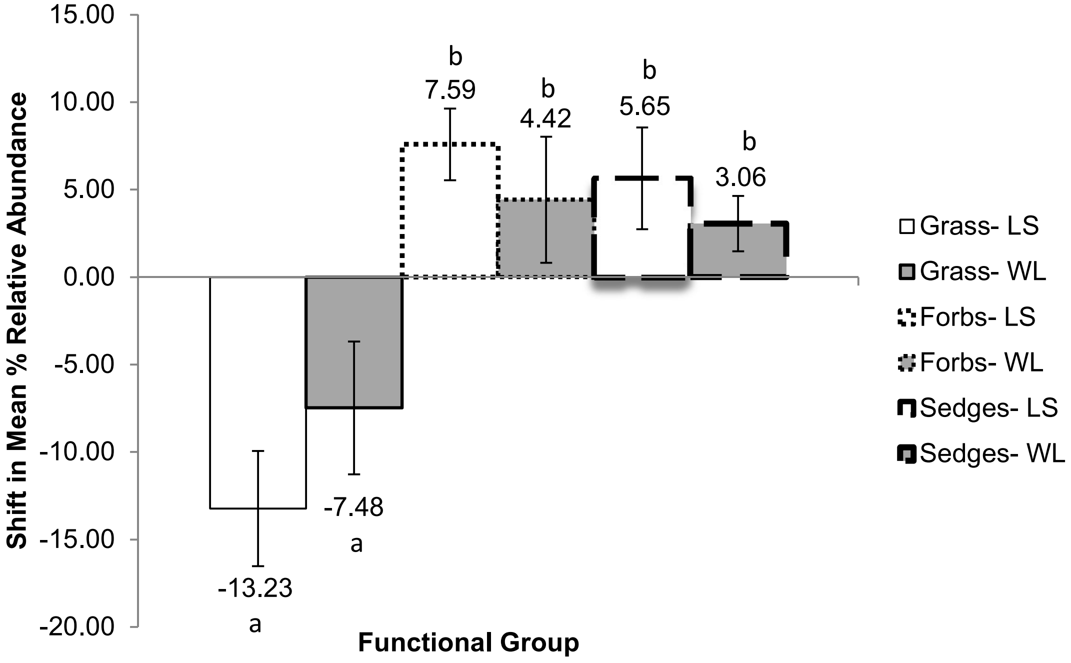


Figure 4b.

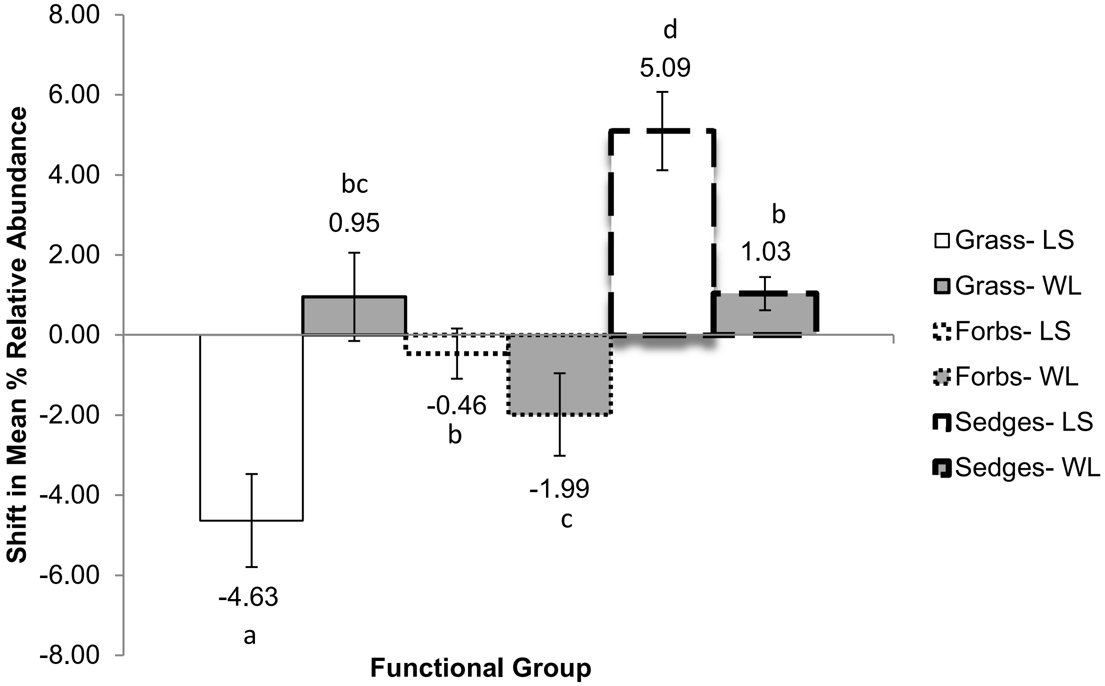


Figure 5a.

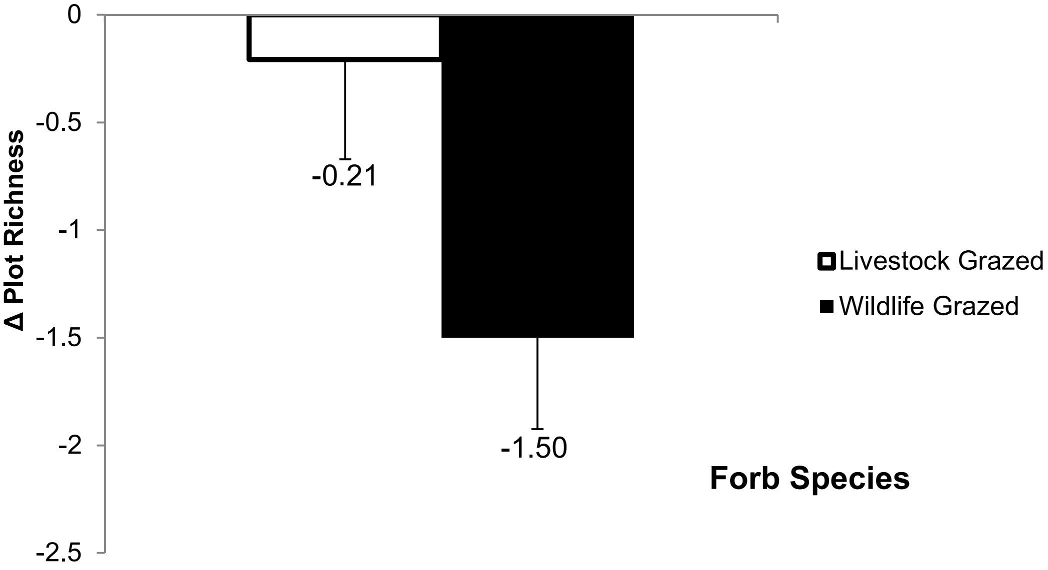


Figure 5b.

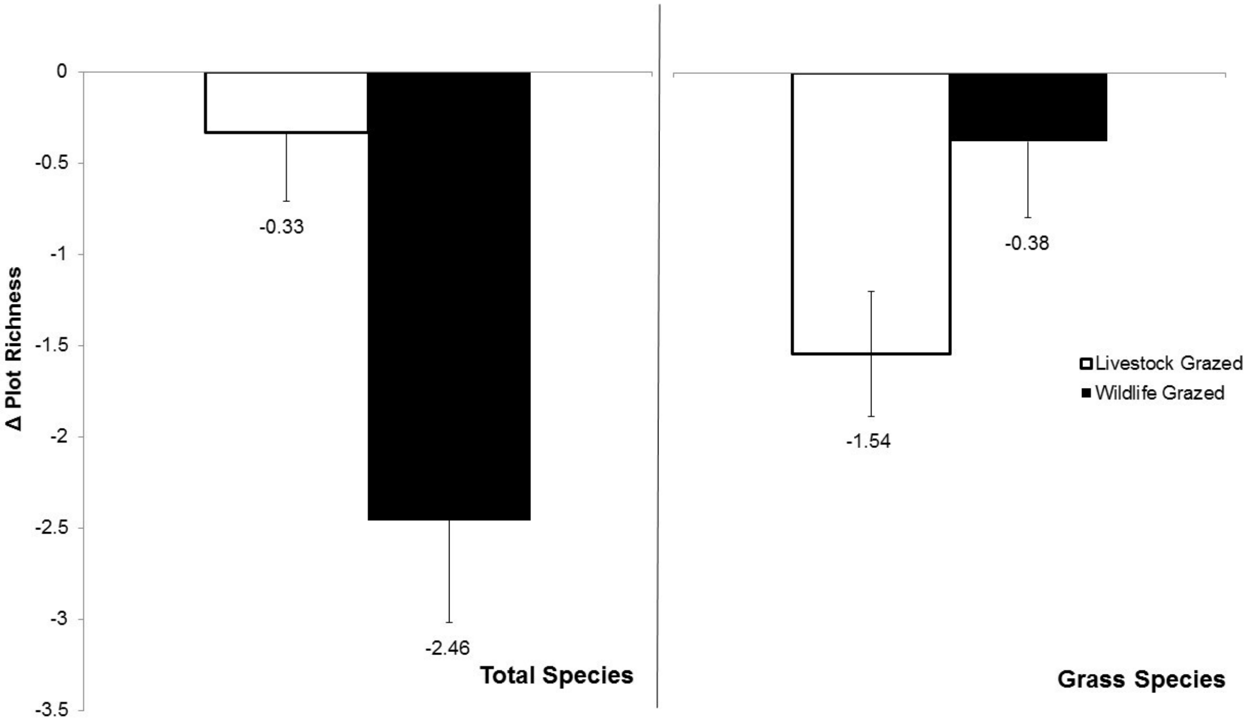
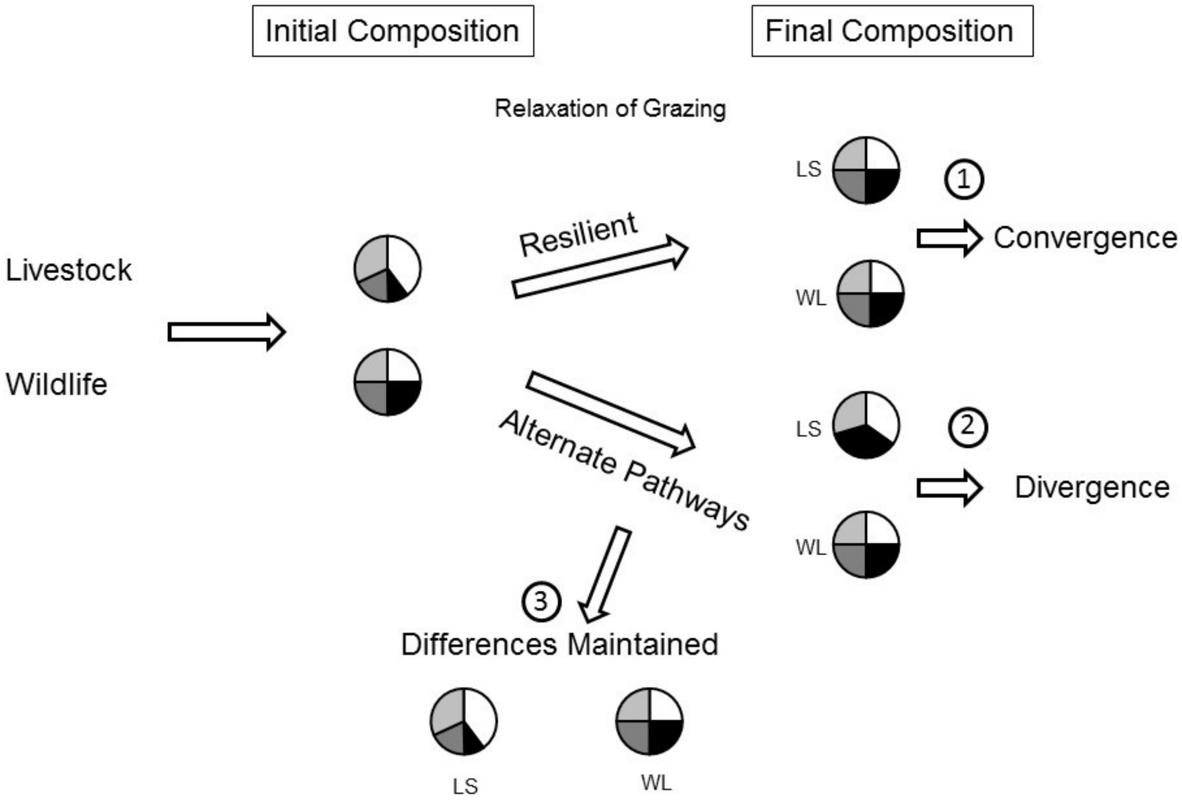


Figure 6.


Initial Composition
Final Composition
Relaxation of Grazing
Livestock
Wildlife
Resilient
LS
WL
①
Convergence
Alternate Pathways
LS
WL
②
Divergence
③
Differences Maintained
LS
WL

CHAPTER 3

The where and why of livestock movement patterns: understanding herder decision-making in an agropastoral context

ABSTRACT

Free-ranging animal movement (or lack thereof) is one of the key differences between native and domestic ungulate grazing strategies. This is because domestic livestock movements are controlled by a human manager whose decisions are constrained by a host of physical (Coppolillo 2000; Adriansen & Nielsen 2002; Scholte *et al.* 2006) and socio-economic (Coppolillo 2000; Baker & Hoffman 2006) constraints, as well as potentially by various perceptions they hold regarding aspects of their environment (Baird *et al.* 2009). This difference in mobility across native and domestic systems is significant as grazer movement strategies affect the spatial pattern, and thereby potentially the magnitude and direction, of grazer impacts on a variety of ecosystem properties (Illius & O'Connor 1999), and could play a role in why grazing by native herbivores may positively affect ecosystem properties while grazing by domestic stock often does not (McNaughton 1984, 1986, 1993). Thus, in attempting to understand differences in grazer impacts, it becomes necessary to understand the broader context within which decisions by managers of domestic animals are made. This study uses questionnaires (n = 31) to uncover the various environmental, socioeconomic and other influences on herder decisions regarding herd management and movement within two sub-villages surrounding the Serengeti ecosystem of northern Tanzania. Results reveal that while the search for water and forage resources consistently ranked as the highest concern when making movement decisions, a

host of other factors, such as herd size or whether livestock are kept for subsistence or commercial purposes, play a role in decisions such as whether to leave the village area or to enter illegally into a protected area for grazing. These results further reveal the necessity of recognizing the larger historical context in which agropastoral communities are set in order to better comprehend regional differences in decision-making. Understanding the context in which herd movement decisions are made can reveal clues into the drivers of grazer impacts on ecosystem properties, such as a system's resistance to or propensity for plant compositional change (Chapter 2).

INTRODUCTION

Grazer movement strategies and resulting spatial patterns of grazing can affect grazer impacts on a variety of ecosystem properties (Illius & O'Connor 1999), including species composition (Augustine & McNaughton 1998), diversity (Hart 2001; Hickman *et al.* 2004), primary production (Hobbs *et al.* 1996), nitrogen cycling (Hobbs *et al.* 1996), and rates of soil carbon storage (Sanjari *et al.* 2008; Steffens *et al.* 2008). In fact, freedom of movement and migratory behavior have been suggested as reasons why grazing by native herbivores may positively affect ecosystem properties while grazing by domestic stock may not (McNaughton 1984, 1986, 1993). Furthermore, herding and other livestock husbandry and management practices have the potential to alter the effects of domestic ungulates on plant resources and significantly increase the number of herbivores supported by a given level of production (Oesterheld *et al.* 1992). Thus, it is reasonable to expect that differences in the way herbivores move (or are moved) across the landscape could have a profound influence on their effects on ecosystem properties and particularly, how these effects are distributed spatially.

Free-ranging animal movement (or lack thereof) is one of the key differences between native and domestic ungulate grazing strategies. This is because domestic livestock movements are almost always controlled by a human manager- be it a farmer or manager who encloses them in a limited area through fencing or a herder who directly or indirectly guides the direction and pace of their movement across a landscape. So while free-ranging, wild herbivore movement decisions are driven primarily by the constant search for high-quality forage (Avgar *et al.* 2013) and access to water and minerals (as well as predator avoidance and social activities (Plumb & Dodd 1993)), livestock movement decisions are often constrained within the decisions of human managers. Human managers can be limited in their decision-making by a host of physical (Coppolillo 2000; Adriansen & Nielsen 2002; Scholte *et al.* 2006) and socio-economic constraints (Coppolillo 2000; Baker & Hoffman 2006), as well as potentially by various perceptions they hold regarding aspects of their environment (Baird *et al.* 2009), such as local population density or perceived competition for resources, and the risks of grazing in one place versus another (Bollig & Schulte 1999; Ayantunde *et al.* 2000). These factors that motivate individual herder choices on herd movement could play a significant role in herders' ability to sustainably manage livestock and prevent environmental degradation (Turner & Hiernaux 2002; Baker & Hoffman 2006). Understanding these motivations may thus present a key component of the spatial distribution of livestock and their impacts on the ecosystem. Investigating how these factors affect variation in movement across herds is important, as individual herders have been found to make significantly different decisions regarding herd mobility even when facing similar ecological conditions (Baker & Hoffman 2006).

Physical constraints on herd movement might include herd size and number of herds, with bigger herds requiring herders to travel farther (Butt 2011) and more divided herds requiring more herders; number of available herders (Butt 2011), which could subsequently affect herd size and thus, distances travelled; and access to different resources, such as fields with crop residues. Socio-economic constraints that may influence how a herder decides when and where to move his/her animals for grazing could include gender, age, livelihood sources, education level, and family size, as well as whether a herder is a lifelong resident of the area or has immigrated there. Factors such as whether a livestock owner herds his stock separately from other owners or joins up to herd together, whether a livestock owner has access to non-relative herders, and how a livestock owner obtains information about distant grazing sites might also influence herd movement patterns (Turner *et al.* 2014). Lastly, how herders decide when and where to move their herds for grazing might depend on their individually-held perceptions of their environment: of human and livestock population density, which affects their perception of the size and quality of grazing area available to them; of the risk of transmission of disease from wildlife, which could influence the direction of movement (towards or away from wildlife-visited areas); and of the perceived risk associated with grazing illegally in a protected area, which might influence their likelihood to do so, as well as affect the direction and distance of grazing area available to them as potential options for movement.

This study used in-depth questionnaires to explore the influences of each of these three components (physical, socio-economic, and perceptions) on individual herder movement and management decisions and compared across two regions surrounding Serengeti National Park, Tanzania. Both regions are comprised of a mix of ethnic groups practicing agropastoralism, *i.e.* some combination of agriculture and livestock-keeping, in open village areas constricted in size due to 1) their location immediately adjacent to a natural protected area and 2) an increasing density of smallholder farms. Thus, this study also assessed whether variation in any of the above factors is related to livestock owners' self-reported likelihood of illegally grazing herds within a protected area.

I expected that herding strategies in both regions would be limited due to a variety of ecological, economic, political, and socio-cultural factors but that a primary factor would likely be restrictions of herd movement caused by 1) access to a limited grazing area and 2) the need to locate grazing movements around the area accessible from home (Coppolillo 2001). The limited grazing area is due firstly to the fact that a dominant livelihood in the study areas is agriculture and therefore, extensive village lands are taken up by farms, which severely restricts grazing during the wet season. Additionally, as mentioned above, all villages in the study areas are located adjacent to a border of a protected area such as a game reserve or national park which, due to the preservation of these areas as natural systems reserved for native wildlife, further restricts domestic herd movement year-round. However, the degree of this constraint may be tied to herders' *perceived risk* of grazing in protected areas, which relates to enforcement of livestock prohibition policies and may, for those individuals perceiving little to no risk, increase the realized size of available grazing area. Acknowledgement of these restrictions is important because they dictate the size of the area in which herders can make and act out grazing movement decisions.

Secondly, herd movement decisions are limited for agropastoralists by the need to return home with the herd each day, a phenomenon described by Coppolillo (2001) as the 'central-place approach'. Under this approach, resource use is constrained by the need to start and end resource collection at a central place, often the home or farm. This sets a limit on the distance a herd can travel in a day and thus, the number of places a herder can choose to go. Another important factor limiting flexibility in herder decision-making regarding movement is the location of a sufficient and suitable water source. In the dry season at least, I expected this to be a significant factor influencing both the direction and the distance of herd movement in both my study villages, as has been found to be the case in other studies (Coppolillo 2000; Adriansen & Nielsen 2002).

Beyond these two major restrictions on overall herding strategy, I expected that any variation in reported likelihood of grazing in a protected area would be related to variation in herd size, number of available herders, perceptions of human and livestock population density and lastly, perceived frequency of competition over grass and water. I expected that respondents with greater herd sizes and higher numbers of herders available to them would be more likely to graze in a protected area than those with smaller herds and fewer herders. I also expected a higher likelihood of grazing in a protected area from respondents who perceived population density to be high- either of humans, which could indicate a greater concentration of farms in their preferred grazing area and thus, perhaps lead them to seek out additional grazing resources in a protected area,; or of livestock, which could indicate competition over grazing resources and also potentially drive them to other, even illegal, grazing areas. Similarly, I expected a higher likelihood from those who reported experiencing competition over water or grass often.

METHODS

This research was conducted in the Greater Serengeti Ecosystem (GSE) of Tanzania, East Africa, in two regions adjacent to the area known as the 'western corridor' of Serengeti National Park: 1) Kijereshi region, located to the south (Magu District) and 2) Isenye region, located north of the western corridor and neighboring Grumeti Game Reserve (Serengeti District)(purple polygons, Figure 1a). These regions have historically been the lands of the Wasukuma and Waikoma peoples, respectively, though a great deal of emigration from other areas has taken place in recent years (Sinclair *et al.* 2008). Traditionally both groups are agropastoralists, making a living through tending small farms and often a small herd of livestock, primarily cattle with a few sheep and goats. The Wasukuma, Tanzania's largest ethnic group (Coppolillo 2000) and the dominant ethnic group in Kijereshi, are also known for growing cash crops such as rice, maize, or cotton, but for the majority of people in these regions, livestock represent the primary source of wealth (Sinclair *et al.* 2008). However, with a poorly developed road network and consequent limited access to markets, people in these areas are often forced to sell produce and livestock at low prices (Sinclair *et al.* 2008). This, in combination with increasingly unpredictable rainfall patterns, increasing population density, and conflicts with wildlife can make achieving a sufficient livelihood here exceptionally difficult. As a result, many studies have highlighted the tendency for residents of these regions (Serengeti and adjacent Bunda district, in particular) to supplement diet and income with illegal hunting of wildlife (Kaltenborn *et al.* 2005; Nyahongo *et al.* 2005; Knapp 2007; Sinclair *et al.* 2008).

Within these regions, I concentrated on two sites: the village of Iharara, along the northern border of Grumeti Game Reserve, in the Isenye ward of Serengeti District; and the village of Lukungu, lying at the confluence of the southern border of the western corridor of the national park and the southern and western borders of Kijereshi Game Reserve, at the edge of the GSE and the tip of Speke Bay, Lake Victoria, near the town of Lamadi in Magu District (Figures 1a, 1b). The villages of Iharara and Lukungu are comprised of 369 and 547 households supporting 4,137 and 2,532 people, respectively, according to recent census data (Table 1). Iharara is home to nearly 8,000 livestock, comprised of 49% cattle while Lukungu contains almost 10,000 livestock, of which 70% are cattle.

A focal sub-village within each study village (Nyamisisi within Iharara and Mwamalole within Lukungu) was then selected (Figure 1b) based on the number of livestock owners, total number of livestock, and proximity to experimental exclosure plots for a related study by the author (Chapter 2). Nyamisisi sub-village contained 29% (n = 107) of households in the greater Iharara village (n = 369 total households) and held 36% (n = 2,799 total head) of the total livestock in the village (n = 7,742 total head) (Table 1). Mwamalole sub-village contained only 9.5% (n = 52) of total village households (n = 547 households) yet held 57% (n = 5,500 total head) of Lukungu village's total livestock (n = 9,712 total head) (Table 1). Within each sub-village, livestock owners made up 36% (n = 39) and 52% (n = 27) of households in Nyamisisi (n = 107 total households) and

Mwamalole (n = 52 total households), respectively (Table 1). Cattle were the most common livestock species in both sub-villages, accounting for 59% of total livestock in Nyamisisi and a whopping 91% of all livestock in Mwamalole.

Both sub-villages lie within sizable grassland areas (~10,000 - 20,000 ha) and adjacent to the borders of protected areas where wildlife graze predominantly inside the protected area and livestock graze directly outside (Figures 1a, 1b). While the protected areas are not fenced, each border (excepting those marking Kijereshi GR, which is open) is delineated by a major river which discourages (although does not make impossible, especially in times of low water flow) the passage of either group of herbivores. Humans and their livestock are further deterred from entering the protected areas by the presence of nearby ranger posts in the southern site, the use of look-out points to guide patrols in the northern site, and steep fines if caught at both.

Village grazing areas in both regions are patches of open C_4 grassland dominated by the grasses *Chrysochloa orientalis*, *Sporobolus ioclados*, and *Themeda triandra* (Chapter 2). Mean annual precipitation ranges from 750 – 1,000 mm/year (Sinclair *et al.* 2008) and is seasonal, with the so-called long rains typically falling from March through May and the short rains expected in late October through early December, though the timing and duration of rainfall has become increasingly hard to predict. Soils are primarily sandy clay loams (Chapter 2). Livestock grazing activities in these regions are restricted to daytime hours, with herds enclosed in thornbush bomas (corrals) at night, as predators from neighboring protected areas, such as hyena and leopard, pose a serious threat. However despite nighttime protection within corrals, often supplemented by the use of guard dogs, carnivores do nevertheless occasionally prey on livestock (Holmern *et al.* 2007b).

These areas are ideal to explore the above questions due to the large numbers of year-round resident livestock (primarily cattle) and because they are inhabited by multiple ethnic groups whose sedentary and growing populations are facing increasing pressure to turn already-reduced communal grazing land into more farmland. This phenomenon is likely to have significant effects on the sustainability of livestock-keeping in these areas in the future, as well the impact of livestock grazing on ecosystem function and resiliency.

As mentioned above, these areas have also been the focus of a large body of previous research on topics ranging from human-wildlife and land use conflicts (Kaltenborn *et al.* 2006), including livestock loss to predators (Holmern *et al.* 2007b) and illegal bushmeat hunting (Kaltenborn *et al.* 2005; Nyahongo *et al.* 2005; Holmern *et al.* 2007a; Knapp 2007; Nyahongo *et al.* 2009), to conservation attitudes (Kideghesho *et al.* 2007) and economic incentives of conserving wildlife (Kideghesho 2008). Generally, these studies have found that communities surrounding the western Serengeti have been and continue to experience increasing human population densities which are leading to increasing pressure on limited resources and in turn, greater threats to wildlife (Knapp 2012). This means that villagers in this region are likely to have previous exposure to researchers, both Tanzanian and foreign, and may have even been the subject of previous sociological surveys or other studies aimed at understanding human behavior in this system.

Thus in order to avoid duplicating efforts of previous researchers and to help target survey questions to those issues most relevant to each particular community, a series of initial focal interviews with key informants were conducted in the early dry season of 2010. Village offices were also visited to obtain census data and gain the appropriate permissions. Subsequently and using information gleaned from these interviews, a questionnaire (Supplemental Information S2), comprised of a combination of multiple choice, ranking, and open-ended questions, was developed for use with individual respondents. The variety of questions aimed to uncover what ecological, socio-economic and other factors influence individual herder decision-making in moving livestock around for grazing. Livestock owners were asked to rank the importance of factors such as distance to water, presence or absence of other animals, and vegetation characteristics in determining suitable grazing areas for livestock. In addition, respondents were asked questions regarding daily livestock movement and general perceptions on factors related to the area's suitability and sustainability for livestock grazing, among other things (Supplemental Information S2). Individual livestock owners were surveyed in order to capture variation across households in those socio-economic constraints and beliefs/perceptions that might influence decisions regarding livestock movement and management strategies (Baker & Hoffman 2006).

Individual questionnaires were conducted during the late dry season of 2010 for Mwamalole and through the wet season of 2011 for Nyamisisi. A combination of convenience and random sampling (Fink 2009) was used to select a sample of households to be surveyed within each sub-village. Potential respondents were approached at their respective households and given a brief introduction to both the researchers and the aims, methods, and expected output of the study (Supplemental Information S3). Livestock owners were then invited to participate and informed of the anonymous and voluntary nature of the questionnaires. Participants were also informed that while the researchers found no foreseeable risk to their participation, that they could end participation at any time (Supplemental Information S3). This information was dictated to participants in Kiswahili (the lingua franca of the country and region) and participants given a written copy (Supplemental Information S4). Finally, participants' oral consent was obtained prior to beginning the survey.

Surveys were conducted orally, with the aid of a translator, in Kiswahili and responses were recorded by hand and kept anonymous. Participants were 18 years of age or older and either owned, or belonged to a household that owns, livestock. Only one individual per household (usually the livestock owner/head of household) was surveyed but answers contributed from other household members present during the interview were also recorded. The individual surveyed was either the primary decision-maker regarding herd movement or if the primary decision-maker was unavailable, the individual surveyed was someone with adequate knowledge of how herd movement decisions are made (usually another member of the family responsible for herding). Approximately 35% of livestock owners (n=18) in Nyamisisi sub-village of Iharara in Serengeti District and 52% of livestock owners (n=13) in the Mwamalole sub-village of Lukungu, Magu District were surveyed.

Global Positioning System (GPS) coordinate points were taken of housing structures within the surveyed sub-villages. These points were then plotted in a Geographic

Information System (GIS) using ESRI ArcGIS® v.10.2 software (ESRI 2008) to create maps of population density and distribution within these two areas and to illustrate villagers' proximity to the open grazing area.

Survey data was converted to an enumerative format through the use of coded variables and then analyzed in Microsoft Excel (2007) and using the Hmisc package (Harrell Jr. 2014) of the statistical program R (R Core Team 2014). Summary statistics were used to assess variation in individual responses. Statistical tests included Pearson's correlations (*rcorr* function in R) for quantitative variables and Fisher's exact tests (*fisher.test* in R) for categorical variables.

RESULTS and DISCUSSION

Socio-Economic Data

A total of 31 questionnaires were conducted with 42% of these coming from the focal sub-village of Mwamalole within the Kijereshi study region (n=13) and 58% coming from the focal sub-village of Nyamisisi within the Isenye study region (n=18). Of the 31 respondents, 90.32% were male (100% male in Mwamalole, 83.33% male in Nyamisisi) and 51.61% were of the Sukuma ethnic group (Table 2). Other ethnic groups represented in the sample included Mkuria and Msweta in Mwamalole and Isenye, Tatulu and Seyu in Nyamisisi. The largest share (32.26%) of respondents were between the age of 40-49, followed closely by 20-29 year olds (29.03%) and finally by those between the age of 30-39 (19.35%) and those over 49 years old (19.35%, Table 2). A large number of respondents had completed primary school (45.16%) or attended some primary school (29.03%), while fewer had no formal education at all (22.58%) and only one respondent (3.23%) had reached secondary school (Table 2). Respondents' family size ranged from 3-27 individuals, with an average of 12 people per family (Table 3).

The majority of participants were agropastoralists who engaged in both agriculture and livestock keeping (80.65%) while a small number (9.68%) combined agropastoralism with some external venture (such as a business or an outside job) and another small group (9.68%) kept livestock as their sole livelihood (Table 2). Most respondents (74.19%) kept livestock for the purpose of subsistence while roughly one quarter (25.81%) used them for commercial purposes as well (Table 2). Respondents in Mwamalole were more likely to use livestock for commercial purposes (53.85%) than in Nyamisisi (5.56%, Table 4). Finally, a greater number of respondents (54.84%) had immigrated to the area in which they were surveyed at some point in their life than those (45.16%) that were lifelong residents of the area (Table 2) and this was the case primarily in Mwamalole where 76.92% of respondents were immigrants (compared to 38.89% in Nyamisisi, Table 4).

Herd Management Data

Herd sizes varied greatly among respondents, ranging from 8 animals to approximately 2,120 animals and averaging 177 animals per herd (SE = 68). The largest share of respondents (25.81%) had a herd size between 21 and 50, with a mode of 44 animals per herd (Table 3). Herd size was significantly correlated with family size (n = 31, $r = 0.46$, $R^2 = 0.208$, $p = 0.010$), with those respondents with larger families also having larger herds. This association was significant even after removing the outlier of one particularly large herd (n = 30, $R^2 = 0.169$, $p = 0.024$, Figure 2). These numbers also differed somewhat by region, with more large and small herds in Mwamalole where the biggest share of respondents (30.77%) held herds of between 201 and 500 animals followed by those with herds of 0-20 animals (23.08%) and 21-50 animals (23.08%) per herd, while in Nyamisisi, most respondents had medium-sized herds under 200 animals (27.78% of respondents each held 21-50, 51-100, or 101-200 animals per herd). Thus, livestock keepers in Mwamalole tend to be either those with small holdings used primarily for milk and farm labor or those with very large holdings used for commercial purposes. In Nyamisisi, on the other hand, medium-sized herds tend to be the norm with very few respondents having less than 20 animals or greater than 200, indicating a more typical pastoral or agropastoral lifestyle. Herds were made up primarily of cattle in both regions, with an average of 132 ± 65 cattle per herd, followed by a mean of 27 ± 7 sheep and 19 ± 6 goats per herd (Table 3). There were no significant differences in mean numbers of cattle, sheep or goats across study sub-villages.

The number of herders used reported by respondents ranged from 2-10 and averaged 4.45 ± 0.38 per homestead (Table 3) and was correlated with both family size ($n = 31$, $r = 0.40$, $R^2 = 0.162$, $p = 0.025$, Figure 3) and herd size ($n = 31$, $r = 0.36$, $R^2 = 0.130$, $p = 0.046$, Figure 4). However, the relationship with herd size was no longer significant after removing the outlier of one particularly large herd ($n = 30$, $R^2 = 0.051$, $p = 0.230$). Only twenty-nine percent of respondents reported using a non-relative (*i.e.* hired) herder and only sixteen percent said they herd their animals together with another livestock owner (Table 5). Whether or not sheep and goats were herded separately from cattle was different across regions, with seventy percent of owners in Mwamalole reporting yes and eighty-eight percent of respondents in Nyamisisi reporting no (Table 4).

Almost all respondents reported that the herder is the one who makes the daily movement decisions for the herd, with livestock owners reporting themselves as the ones directing them in less than ten percent of participants. Respondents' estimated average total daily distance travelled by herds (from the time they leave home in the morning until they return in the evening) ranged from 4 – 40 kilometers with a mean of 12.87 ± 1.28 km and a mode of 10 km (Table 3). The estimated maximum distance from home travelled by herds ranged from 1.5 – 25 kilometers with a mean of 5.79 ± 0.75 km and a mode of 5 km (Table 3). These estimates did not differ significantly across regions and were not significantly associated with any other variables and this is believed to potentially be due to the figures being rough estimates made by respondents without the use of a map or other aid in determining accurate distances.

All respondents described the daily movement pattern as moving herds around from place to place as needed based on vegetation quantity. Respondents were asked about the importance of various vegetation characteristics when making herd movement decisions and vegetation quantity was listed as very important by one hundred percent of respondents. Vegetation density was the second most-cited as very important (90.32%), followed closely by vegetation height (87.10%) and vegetation type (77.42%). Just under sixty-five percent of total respondents cited vegetation color as very important, while only fifty percent reported vegetation quality to be very important. Several respondents commented that cattle don’t like to eat tall grass or that it is bad because it hits the animals in the eyes or can hold ticks or hide predators. Respondents also mentioned that denser vegetation is preferred, at least in the dry season, when sparse vegetation patches can make the animals harder to look after and as dense vegetation allows them to stay longer and requires less moving around from place to place. As for vegetation type, several mentioned that there are certain types of grass that cattle don’t like and some that can make them sick but, as one respondent said, “if you know what [species] are there, can send even the kids to go [as herders]!” When asked how vegetation quality is assessed, a variety of answers were given but most responses centered around grass that was either bright or dark green and of short or medium height.

Beyond vegetation characteristics, another factor that makes an area good for grazing is temperature as hotter areas were said by a few to be preferred by both herders and animals. Factors that make an area bad for grazing included areas with dangerous animals/predators; areas with insects/ticks; a high density of cattle (particularly if the animals are using the area every day which could “turn the area into a desert”); dust, which can make cattle sick; erosion, which has lowered the favorability of formerly ‘good’ areas; and lastly, as one respondent put it, “where you’re not allowed is bad”. In fact, two-thirds of respondents listed a protected area as a factor restricting movement as these are areas they are not allowed to move through with their livestock. One respondent noted areas near gates and ranger posts of protected areas were especially bad, likely due to the increased change of being caught if grazing inside a protected area.

Other factors that were given as restricting movement included people protecting areas to grow grass for roofs or for their own animals in the dry season; people preventing access to their yards/around their house and to farms, particularly in the wet season when crops are there (in Nyamisisi, several people mentioned that a law prevented this or cited the conflicts that arise when cattle do pass through farms and eat crops); areas that people own (*i.e*. for commercial purposes); disease; wild animals; tsetse flies; thieves; and finally, regulations that prohibit herders from grazing in certain other villages. The majority of herd owners (87.10%) reported that they do not leave the village area for grazing and this was similar across regions (Table 5). Leaving the village area for grazing was associated with the number of herders a livestock owner used, with those who reported leaving the village area having a significantly higher mean number of herders (n = 31, $p = 0.021$, Figure 5).

Most respondents mentioned that grazing around the homestead was usually reserved for sick and young animals that do not go out with the herd but some also mentioned that herds will graze around the house in the mornings a little before heading out or if a herder only has a few animals, they may stay nearby the whole day. Once crops are harvested, farm plots are also used to graze animals, unless otherwise prohibited. One hundred percent of respondents in Mwamalole reported having access to crop residues in the dry season, while just under sixty-five percent did in Nyamisisi.

About half the respondents (n = 16) agreed that the main difference in grazing patterns or herding practices between seasons is that they must travel farther during the dry season than in the wet. Other responses were varied depending on the region and on the individual respondent's location within the village. As mentioned above, grazing on crop residues/farm plots takes place only in the dry season and several respondents in Nyamisisi (n = 3) claimed that this was possible only on their own farms, not others. Another common response (n = 8) was that in the dry season, they will go "anywhere there is grass". In the wet season, one respondent mentioned that swamps and drainage areas must be avoided because there can be too much water while another said that he grazes on top of hills in the wet season because of mud. Several respondents in Nyamisisi (n = 8) said that they only go south in the wet season (towards river/away from farms) but others mentioned they might not reach the Rubana in the wet season, as there is usually enough water around. Another said that he travels south to the Rubana in both seasons. A few others (n = 3) also said that they can only go south in the dry season as well, as there are villages in all other direction. One respondent in Nyamisisi mentioned that in dry he will go towards, and sometimes inside, the game reserve (Grumeti).

In Mwamalole, some respondents (n = 3) said that in the dry season, they will go north (towards the national park and Kijereshi game reserve) and in the wet season, they will go everywhere because water is plentiful and ubiquitous. Others (n = 5) said that in the dry season, they go in the direction of water; while in the wet season, they must move away from/avoid farms. Several (n = 3) mentioned that in the wet season, avoiding farms meant going to the north, which is also where they would get water from the river. Two respondents said that in the dry season, they go just to the lake and back. Finally, one respondent said that there are no seasonal differences, as he always goes towards the national park and/or game reserve.

One respondent from Mwamalole said that, in the dry season, they will take their large herd to graze inside the national park and camp inside for up to three weeks if they can manage to stay undetected. If they travel far, only the animals who have babies or need medicine will return home each day. However, in the wet season, according to this respondent, all animals come home at the end of each day.

Herder Perceptions

Half of all respondents perceived human population density to be moderate, while another forty percent saw it as high or very high and only ten percent characterized it as low (Table 6). These figures differed slightly by region however, with more respondents in Nyamisisi perceiving the human population density as high or very high (50.00%) than in Mwamalole (25.00%) (Table 4). All respondents (n = 31) from both regions agreed that there were more people living in the area now than when they arrived. This was attributed almost equally to an increase in family size and to immigration of people from other areas.

Most respondents (n = 25) agreed that there are more livestock in the area now than in the past and this was attributed to a variety of reasons, including a lower incidence of mortality from disease, an increase in both the number of people keeping livestock and the number of animals kept, immigration of people with their livestock into the area, and a concentration of people settling with their livestock in the area due to farming ties (as opposed to historically migrating in and out of the area seasonally). The majority (58.06%) of all respondents saw livestock population density as high or very high, followed by another thirty-five percent who characterized it as moderate (Table 6). This perception was significantly related to age (n = 31, $p = 0.003$), with older respondents (> 40 years) more likely to characterize it as high or very high and younger ones from 20-29 years the only group to see it as low (Figure 6). As a result, most respondents (80.65%) did not think livestock-keeping would be successful in the area (Table 6). Another ten percent replied that they did not know, while fewer than ten percent said yes. Responses were similar across regions but more doubtful in Mwamalole where not one single respondent thought future livestock-keeping could be successful. The most common reason given (n = 29) for the failure of future livestock-keeping in the area was the shrinking grazing area that is seen as becoming insufficient, or as one respondent put it "all cattle will be finished because where will you feed them?". This was attributed to the increase in the number of people, houses, and cattle and in the area of farms, as well as to the already limited space due to the protected areas.

Despite this, very few respondents (7.69% in Mwamalole and 27.78% in Nyamisisi) stated that they experience competition over grass often (Table 6) with the majority in both regions having reported experiencing it rarely (50.00% in Nyamisisi) or not at all (69.23% in Mwamalole) (Table 4). In Nyamisisi, some noted this competition occurs primarily during the months when the wildebeest migration is nearby. Perception of competition over water, however, was starkly different across regions (Table 4). One hundred percent of respondents in Mwamalole reported that they never experienced it, while in Nyamisisi, the majority (66.67%) of respondents reported experiencing it often. This perception was also significantly associated with the purpose for which livestock was kept (n = 31, $p = 0.001$) with those who keep livestock for subsistence purposes only more likely to report experiencing competition for water than those who keep livestock for both subsistence and commercial purposes. Water competition in Nyamisisi was also associated with times when wildebeest are present and noted to be worst during the dry season. The majority of respondents in both regions agreed that water availability is a big problem in the dry season but that in the wet season, there is usually enough. In Mwamalole, 84.62% reported going to Lake Victoria for water (or using other small ponds nearby), while the remaining used a river (either the nearby Lamadi River or the Mbalageti at the border of the national park). For some, the problem in the dry season was the far distance of the lake (approximately 5 km). In the wet season, the majority (69.23%) begin going to a river. In Nyamisisi, on the other hand, 94.44% of respondents reported taking their livestock to a river during the dry season (primarily the Rubana River south of the village along the border with Grumeti Game Reserve, though some mentioned occasionally visiting the Tirina River to the west (Figure 1)) and this number decreased to only 61.11% during the wet season, when some reported watering their animals from ponds and swamps nearby the homestead. In all cases, most respondents reported that animals were brought to water once a day.

Perception of risk of disease from wildlife also varied with region (Table 4), with respondents in Nyamisisi perceiving greater risk than those in Mwamalole. In Nyamisisi, most respondents (72.22%) perceived the risk as high or very high, followed by another 22.22% who saw it as moderate. In Mwamalole, on the other hand, the greatest share of respondents saw disease from wildlife as a small risk (38.46%), while only 23.08% saw it as high or very high and another 23.08% as moderate. Across regions, this perception was related to age ($n = 31$, $p = 0.015$), with older respondents (> 40 years) more likely to perceive a big or very big risk and younger respondents (< 40 years) more likely to perceive no risk at all. In both regions, one hundred percent of respondents said that they used vaccinations and dipping as preventative measures against diseases from wildlife. Another strategy was keeping livestock herds separate from wildlife with most (64.00%) respondents saying that they keep their animals a minimum distance of 200 or more meters from wildlife herds (Table 6). Respondents in Mwamalole keep their herds farther from wildlife than those in Nyamisisi, with 85.71% staying more than 200m away, while the remaining 14.29% stay at least 100 meters from wildlife. In the Isenye region where Nyamisisi is located (Figure 1), wildlife and livestock come into closer contact more frequently when wildlife cross the Rubana River into the village grazing area, and hence only 55.56% respondents say they stay a minimum of 200 meters away, with another 16.67% staying at least 100 meters, 16.67% staying between 50-100 meters, and 11.11% of respondents saying they will let their herds get as close as 0-10 meters. In Mwamalole, most respondents agreed that most conflicts with wildlife are rare because the wildlife usually stays far or people will intentionally keep their animals separate.

Eighty-three percent of total respondents reported that the risk for illegally grazing inside a protected area was big or very big (Table 6), though respondents in Nyamisisi were slightly more likely to think so, with 94.44% reporting this level of risk compared to 66.67% in Mwamalole. The remaining respondents in Nyamisisi classified the risk as moderate and while 25% of those from Mwamalole agreed, a further 8.33% reported the risk as small. The most commonly cited risk of grazing in a protected area was that of getting caught and having to pay a fine (n = 26), followed by the risk of predators (n = 14). Other risks noted were disease, especially from ticks, tsetse flies or parasites; the risk of injury to animals or the herder himself if caught by rangers; the risk of losing animals or having them get caught up with wildebeest herds; animals getting caught in snares; risk/fear of meeting poachers; snakebite; and finally a few mentioned how the long grass often found in protected areas can damage/irritate the animals' eyes.

To Go or Not to Go: Grazing in Protected Areas

Approximately forty-five percent of total respondents reported that they were not at all likely to graze herds in a protected area, followed by about nineteen percent who said they were somewhat likely and another nineteen percent who said they were only likely to a bad dry season (Table 6). Sixteen percent overall said they were very likely to graze in a protected area. These responses were different across regions (Table 4), with respondents in Mwamalole reporting themselves more likely to graze in a protected area. Here, only 7.69% of respondents said they were not at all likely to graze in a protected area, while the remaining were split equally between very likely, somewhat likely, and only likely during a bad dry season. In contrast, respondents in Nyamisisi overwhelmingly (72.22%) reported that they were not at all likely to graze in a protected area, while only 5.56% said they were very likely. Vegetation quantity, distance to ranger posts and gates, and distance to a water source were all reported as very important factors in deciding whether to enter a protected area to graze. The importance of distance from home, however, was cited as not important by a majority (90.91%) of respondents in Mwamalole, while only 40% of those in Nyamisisi agreed. Another 40% in Nyamisisi thought it was very important while the remaining 20% saw it as somewhat important. This could be due to the fact that in Mwamalole, almost all residents live very near to a protected area while distances from home to the Grumeti Game Reserve vary among residents of Nyamisisi (Figure 1). This could also be attributed to the greater emphasis placed on other risks by those from Nyamisisi, including the high risk of getting caught and having to pay a steep fine, an issue that didn't seem to be as big of a deterrence in Mwamalole.

As expected, the likelihood of grazing in a protected area was associated with herd size, with those respondents who reported that they were very likely to take the risk of grazing illegally having significantly larger herds than those who were less likely ($n = 31$, $p = 0.011$, Figure 7). This trend held up even after removing an outlier of one particularly large herd ($n = 30$, $p = 0.002$). The purpose for which livestock was kept was also related to a respondent's likelihood of grazing in a protected area ($n = 31$, $p = 0.011$), with owners who keep livestock for the dual purposes of subsistence and commercial (*i.e.* for the sale of animals or animal products) more likely to bring their herd to a protected area (Figure 8) than those who keep livestock for subsistence purposes only. Lastly, a respondent's perception of the risk associated with grazing in a protected area was unsurprisingly associated with the respondent's likelihood of doing so ($n = 31$, $p = 0.013$), with 76% of those who perceived the risk to be big or very big reporting that they were not at all likely to graze in a protected area or only likely to during a severe drought and 80% of those who perceived the risk to be small or moderate reporting that they were somewhat or very likely to do so (Figure 9).

In Mwamalole, a respondent's age was associated with his likelihood to graze in a protected area (n = 13, $p = 0.037$), with only those respondents under forty years old reporting that they were somewhat or very likely to do so (Figure 10). In Nyamisisi, a respondent's likelihood of grazing in a protected area was associated with whether or not the respondent reported ever leaving the village area for grazing or not (n = 18, $p = 0.044$), with 92% of those who reported that they were not at all likely to graze in a protected area also having said they do not leave the village area for grazing.

Regional Differences

According to recent censuses, the village of Lukungu (home to Mwamalole sub-village), in Kijereshi region, has a greater number of people, households, and livestock than the village of Iharara (home to Nyamisisi sub-village) in Isenye region (Table 1). Mwamalole sub-village also has a higher number of livestock and a greater percentage of cattle than Nyamisisi sub-village (Table 1). Despite this and although average herd sizes were similar across sub-villages, respondents in Nyamisisi were more likely to perceive a greater risk of disease from wildlife and reported experiencing more frequent competition over grass and water resources (Table 4). Interestingly, respondents in Nyamisisi were also significantly *less* likely to take herds to graze in a protected area. This seems counterintuitive as it might be expected that livestock owners facing (or at least perceiving) a greater degree of competition and pressure on resources might be more likely to risk trying to obtain these resources from prohibited areas. However, this could be due to variation across the two regions in enforcement of livestock prohibition within protected areas, particularly across Kijereshi and Grumeti Game Reserves, which are managed by different entities.

While livestock owners in both regions face pressure from space limitations and potential conflict and/or competition with wildlife, these pressures seem to be stronger in the Isenye region (Table 4). The more recent eviction of pastoralists and agropastoralists in 2000 (Kideghesho 2008) from the area now managed as the Grumeti Game Reserve (established in 1994) and the subsequent arrival (in 2006) of an external management group that exercises much stricter enforcement of grazing policies within the reserve seems to have led to greater constriction of the livestock population in Isenye and potentially, generated greater competition for resources both between different livestock herds and with native wildlife in this area. Transect counts from a related study also found livestock densities to be higher in Isenye than in the Kijereshi region (Chapter 2).

This is in contrast to the Kijereshi region, where, although the available grazing area appears small (Figure 1), a much more lax enforcement of grazing policies within the Kijereshi Game Reserve (also established in 1994) may mean that livestock owners are able to utilize that entire area for grazing their herds and it seems, based on anecdotal evidence, author observations, and Mwamalole livestock owners' self-reported likelihood of grazing within a protected area (Table 4), that this is in fact what many of them are doing. This differing degree of enforcement may create unequal levels of 'realized risk' (as opposed to perceived risk) across the two regions, with livestock owners in Nyamisisi facing greater real risk of punishment (and possibly steeper fines) for illegal grazing than livestock owners in Mwamalole.

It is likely that this differential access to protected areas across the two regions significantly influences herd management and movement strategies, as it not only appears to have affected individual perceptions of disease risk and competition (Table 4), but to also have led to more concentrated, sustained grazing pressure in the open grazing area of the Isenye region. This continuous pressure seems to have produced a plant community that is much more resistant to compositional change, particularly following the relaxation of grazing (Chapter 2).

LIMITATIONS

One limitation of this study is the small number of total respondents. This was due to the difficulty in surveying every individual livestock owner in the community and to restrictions in time that limited sampling to only one sub-village within each village. However, it is believed that the selected sub-villages and the individuals surveyed within each sub-village offer a representative sample of the communities within these regions and that the relatively small sample adequately captures variation in critical variables such as herd size and purpose of livestock ownership.

Another limitation is related to the estimates given by respondents for the average total distance and maximum distance travelled daily with herds. These figures likely contain a reasonable degree of error due to the difficulty for respondents in making accurate estimations without the use of a map and with limited examples of known distance for reference. Additionally, as more than half of respondents had not completed primary school and only one of thirty-one had went on to secondary school, it is likely that respondents may have been unfamiliar with the calculation of distances in meters/kilometers and this may have confounded estimates (particularly the estimate for average total distance travelled in a day, as this requires summing distances of all segments traveled along an often circuitous path in one day). Nevertheless, respondents were all presented the question in the same manner and so any error in their estimation was likely fairly consistent across responses. Furthermore, the mean for respondents' reported maximum distance travelled from home (5.79 ± 0.75 km) correlates almost exactly with results from Butt (2010)'s study of pastoralists surrounding the Maasai Mara reserve of southern Kenya (an extension of the GSE), which found, using GPS collars on herds from seven households, that the herds' maximum distance from home at any given point in the day was about 6km (Butt 2010).

Finally, it must be noted that while the anonymous and therefore presumed low-risk nature of participation was emphasized to respondents at the outset, it is still possible that some responses may have been biased, exaggerated or falsified. This possibility could be due to a variety of reasons including, but not limited to: fear of retribution for illegal activities, hopes of aid or fear of punishment from government entities based on responses, and/or a previous exposure to researchers that may have led to distrust (perhaps particularly of foreign researchers/"outsiders") or conversely, to a possible inclination toward 'telling them what they want to hear'.

CONCLUSIONS

While there were a number of ecological factors influencing the movement decisions of livestock owners and herders in the western Serengeti region, location of a sufficient water source and quantity and quality of grass resources consistently ranked as most important. Nonetheless, a host of socioeconomic factors and perceptions of environmental conditions seem to play a role in decisions such as whether to leave the village area in search of other grazing areas or whether to take the risk of illegally grazing in a protected area. Variation in the degree of enforcement of protected areas and its effect on the size of the realized risk of illegal grazing may also play a role in the decision to enter these areas. Together, these factors have the potential to significantly affect the spatial and temporal distribution of grazing impacts on plant community composition, productivity, soil nutrient cycling and a host of other indirect effects on ecosystem function (Illius & O'Connor 1999).

Understanding how socioeconomic and other factors influence individual herd movement decisions can help to place into context impacts of livestock grazing across the landscape and may be the key to understanding differences in impacts between native wildlife and domestic livestock grazing systems.

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Table 1. Differences in study village and sub-village population figures by region. Estimates were retrieved from village censuses via Village Executive Officers. Censuses were taken in 2009 (Lukungu) and 2010 (Iharara).

Estimate	Kijereshi	Isenye
Village	Lukungu	Iharara
Households	547	369
Total people	4,137	2,532
Livestock owners (percent of households)	71 (12.98)	102 (27.64)
Total livestock	9,712	7,742
Cattle (percent of total livestock)	6,850 (70.53)	3,816 (49.29)
Sheep/goats (percent of total livestock)	2,862 (29.47)	3,926 (50.71)
Sub-village	Mwamalole	Nyamisisi
Households (percent of village total)	52 (9.51)	107 (29.00)
Total people (percent of village total)	NA	886 (35.00)
Livestock owners (percent of households)	27 (51.92)	39 (36.45)
Total livestock (percent of village total)	5,500 (56.63)	2,799 (36.15)
Cattle (percent of total livestock)	5,000 (90.91)	1,639 (58.56)
Sheep/goats (percent of total livestock)	500 (9.09)	1,160 (41.44)

Table 2. Herder responses to categorical demographic and socioeconomic questions. Numbers in parentheses are percentages of total responses across both sub-villages.

Variable	Response	Number of respondents (%)
Gender	Male	28 (90.32)
	Female	3 (9.68)
Ethnicity	Sukuma	16 (51.61)
	Mkuria	2 (6.45)
	Msweta	1 (3.23)
	Isenye	6 (19.35)
	Tatulu	5 (16.13)
	Seyu	1 (3.23)
Age	20 – 29	9 (29.03)
	30 – 39	6 (19.35)
	40 – 49	10 (32.26)
	> 49	6 (19.35)
Education	None	7 (22.58)
	Primary_some	9 (29.03)
	Primary_completed	14 (45.16)
	Secondary	1 (3.23)
Livelihood	Pastoralism only	3 (9.68)

	Agropastoralism	25 (80.65)
	Agropastoralism + external	3 (9.68)
Purpose of keeping livestock	Subsistence	23 (74.19)
	Subsistence & commercial	8 (25.81)
Resident or Immigrant	Lifelong resident	14 (45.16)
	Immigrant	17 (54.84)

Table 3. Herder responses to quantitative questions regarding herd management and family size.

Variable	Mean ± SE	Range	Mode
Family size	11.94 ± 0.95	3 – 27	10
Total herd size	177.32 ± 68.05	8 – 2120	44
Number of cattle	132.13 ± 64.68	3 – 2000	30
Number of sheep	26.58 ± 6.49	0 – 150	--
Number of goats	18.61 ± 6.24	0 – 180	--
Number of herders	4.45 ± 0.38	2 – 10	4
Average total daily distance travelled (km)	12.87 ± 1.28	4 – 40	10
Maximum distance travelled from home (km)	5.79 ± 0.75	1.5 – 25	5

Table 4. Regional differences in most frequent responses to categorical questions (number of responses in the most frequently cited category listed in parentheses).

Variable	Mwamalole (n = 13)	Nyamisisi (n = 18)
Age	20-29 (5)	40-49 (8)
Ethnicity	Sukuma (10)	Isenye (6)
Education	Primary_some (6)	Primary_completed (10)
Purpose for keeping livestock	Subsistence & commercial (7)	Subsistence (17)
Resident or immigrant	Immigrant (10)	Resident (11)
Herd size category	201-500 (4)	21-50 (5) 51-100 (5) 101-200 (5)
Herd sheep & goats separately?	Yes (7/10)	No (15/17)
Perception of human pop. density	Moderate (7/12)	High/Very high (9)
Perception of livestock pop. density	Moderate (6) High/Very high (6)	High/Very high (12)
Frequency of competition over grass	Not at all (9)	Rarely (9)
Frequency of competition over water	Not at all (13)	Often (12)
Perception of disease from wildlife	Small (5)	Big/Very big (13)

Likelihood of grazing in a protected area	Only during dry season (4) Somewhat likely (4) Very likely (4)	Not at all likely (13)

Table 5. Herder responses to categorical questions regarding herd management. Numbers in parentheses are percentages of total responses across both sub-villages.

Variable	Response	Number of respondents (%)
Herd size	0 – 20	4 (12.90)
	21 – 50	8 (25.81)
	51 – 100	6 (19.35)
	101 – 200	6 (19.35)
	201 – 500	6 (19.35)
	> 500	1 (3.23)
Use of a nonrelative herder	Yes	9 (29.03)
	No	22 (70.97)
Herd sheep & goats separately from cattle?	Yes	10 (33.33)
	No	20 (66.66)
Herd together with another livestock owner?	Yes	5 (16.13)
	No	26 (83.87)
Leave village area for grazing?	Yes	4 (12.90)
	No	27 (87.10)
Access to crops in dry season?	Yes	21 (77.78)
	No	6 (22.22)

Table 6. Herder responses to categorical questions about their perceptions of various environmental factors. Numbers in parentheses are percentages of total responses across both sub-villages.

Variable	Response	Number of respondents (%)
Human population density	Low	3 (10.00)
	Moderate	15 (50.00)
	High/Very high	12 (40.00)
Livestock population density	Low	2 (6.45)
	Moderate	11 (35.48)
	High/Very high	18 (58.06)
Success of livestock-keeping in the future?	Yes	3 (9.68)
	No	25 (80.65)
	Don’t know	3 (9.68)
Frequency of grass competition	Not at all	13 (41.94)
	Rarely	12 (38.71)
	Often	6 (19.35)
Frequency of water competition	Not at all	14 (45.16)
	Rarely	5 (16.13)
	Often	12 (38.71)
Where water animals in dry	River	19 (61.29)

season	Lake/pond/swamps	11 (35.48)
	Other	1 (3.23)
Where water animals in wet season	River	14 (45.16)
	Lake/pond/swamps	15 (48.39)
	Other	2 (6.45)
Risk of disease from wildlife	None	2 (6.45)
	Small	6 (19.35)
	Moderate	7 (22.58)
	Big/Very big	16 (51.61)
Minimum distance kept from wildlife	0 – 10m	2 (8.00)
	11 – 50m	0 (0.00)
	50 – 100m	3 (12.00)
	101 – 200m	4 (16.00)
	> 200m	16 (64.00)
Risk of grazing in a protected area	None	0 (0.00)
	Small	1 (3.33)
	Moderate	4 (13.33)
	Big/Very big	25 (83.33)
Likelihood of grazing in a protected area	Not at all likely	14 (45.16)
	Only during bad dry season	6 (19.35)

	Somewhat likely	6 (19.35)
	Very likely	5 (16.13)

FIGURE CAPTIONS

Figure 1a. Maps showing the location of the study regions within the Greater Serengeti Ecosystem of Tanzania in East Africa, with each study region's grazing area demarcated by a purple polygon and the location of each focal sub-village marked.

Figure 1b. Map of the western corridor of the Greater Serengeti Ecosystem with insets showing locations of livestock-keeping households within the focal sub-villages of Nyamisisi (Iharara village, Serengeti District) and Mwamalole (Lukungu village, Magu District).

Figure 2. Even after removing an outlier of an exceptionally large herd, a significant relationship exists between family size and herd size ($n = 31$, $r = 0.40$, $R^2 = 0.162$, $p = 0.025$).

Figure 3. As family size increases, so too does the number of herders a livestock owner has ($n = 31$, $r = 0.40$, $R^2 = 0.162$, $p = 0.025$).

Figure 4. As the number of herders increases, so too does a respondent's herd size ($n = 31$, $r = 0.36$, $R^2 = 0.130$, $p = 0.046$), though this relationship was no longer significant after removing the outlier of one particularly large herd ($n = 30$, $R^2 = 0.051$, $p = 0.230$).

Figure 5. Respondents who reported that they sometimes leave the village area for grazing (n = 4) had a greater number of herders than those who reported that they never leave the village area with their herds (n = 27) ($p = 0.021$).

Figure 6. A respondent's perception of livestock density in the area was related to the respondent's age (n = 31, $p = 0.003$).

Figure 7. Respondents who reported being 'very likely' to go inside a protected area for grazing (n = 5) had significantly larger herds than those who reported being less likely to do so (n = 31, F = 4.52, $p = 0.011$).

Figure 8. Respondents who keep livestock for subsistence purposes only (n = 23) were much less likely to graze in a protected area than those who keep it for both subsistence and commercial purposes (n = 8) ($p = 0.011$).

Figure 9. The majority of respondents (80%) who found the risk of grazing in a protected area to be small or moderate (n = 5) also reported being somewhat or very likely to graze in a protected area ($p = 0.013$).

Figure 10. In Mwamalole sub-village, the reported likelihood of grazing in a protected area was associated with the respondent's age (n = 13, $p = 0.037$), with older respondents reporting a lower likelihood than younger ones.

Figure 1a.

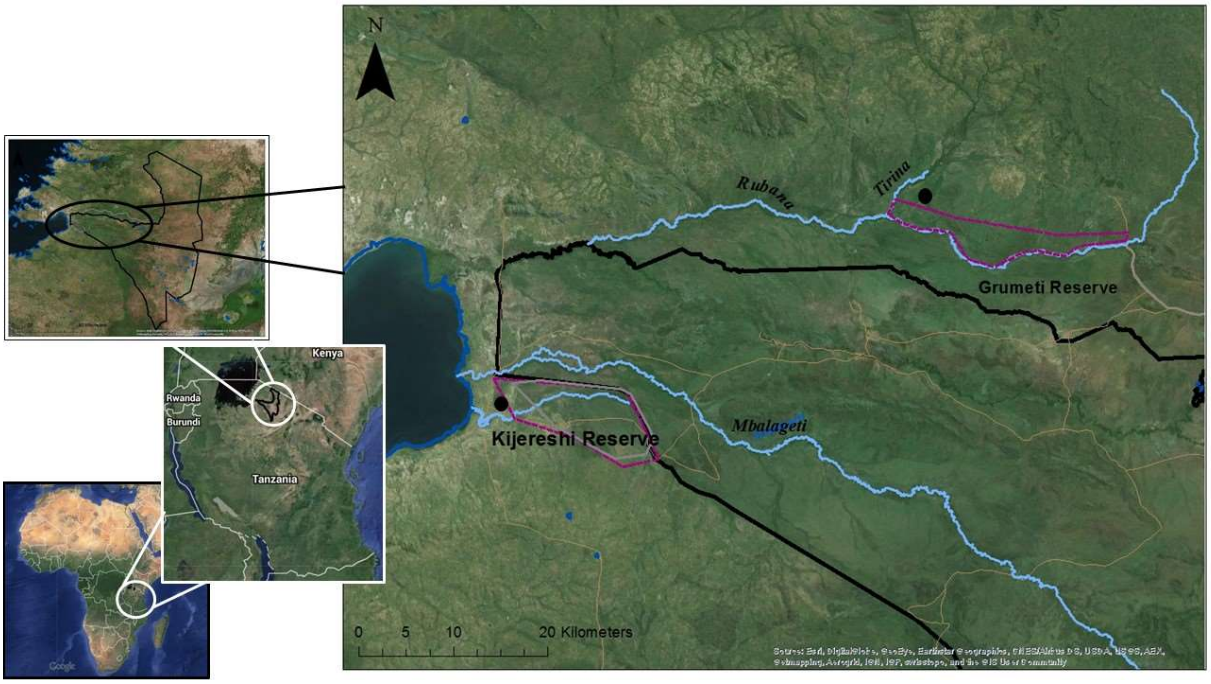


Figure 1b.

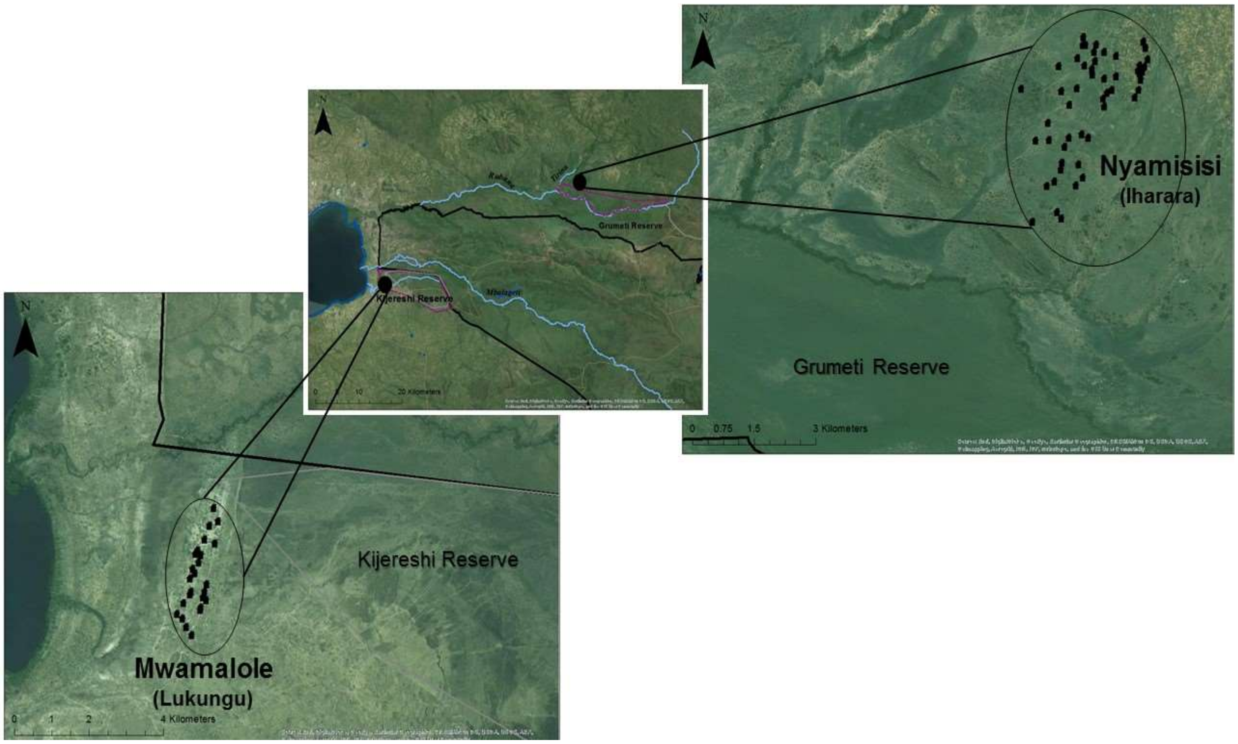


Figure 2.

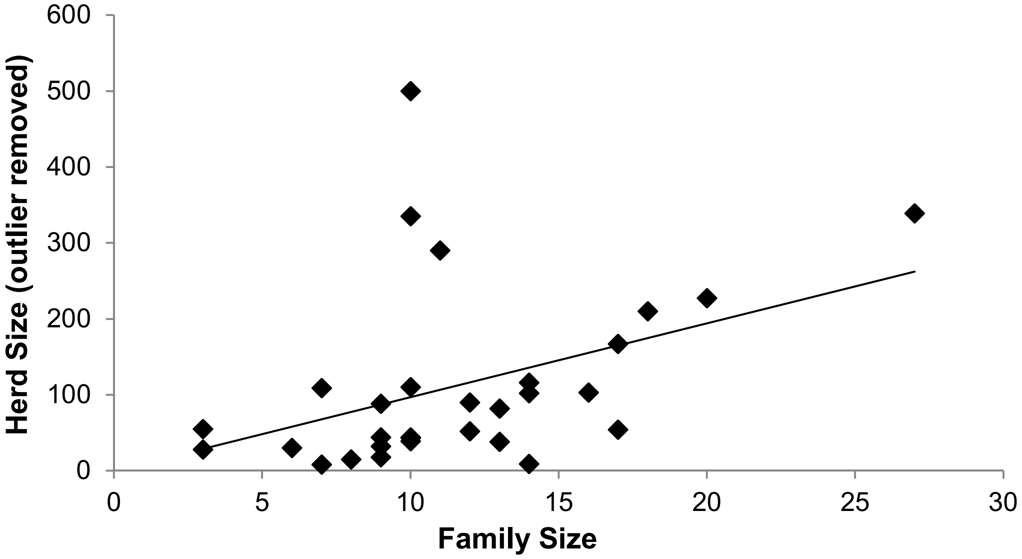
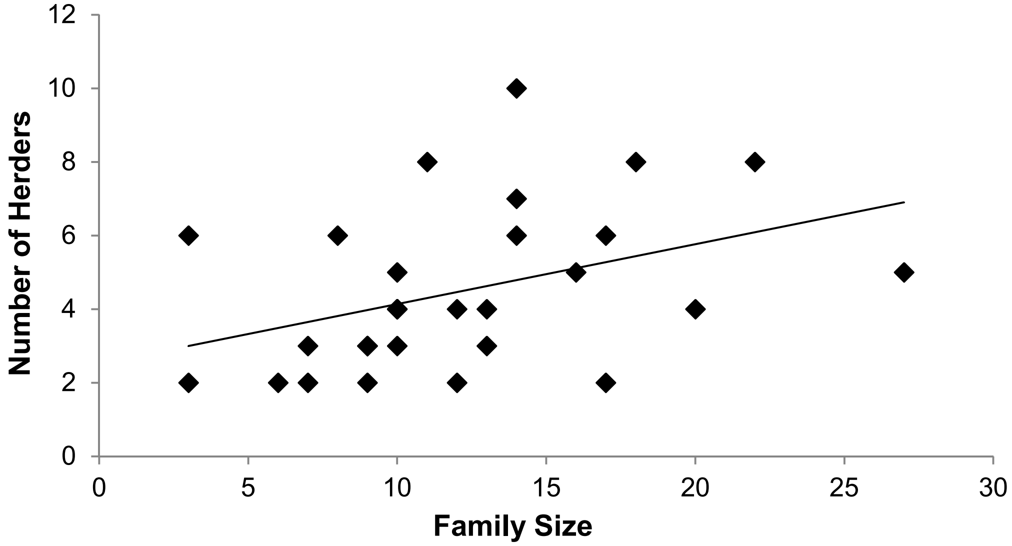


Figure 3.



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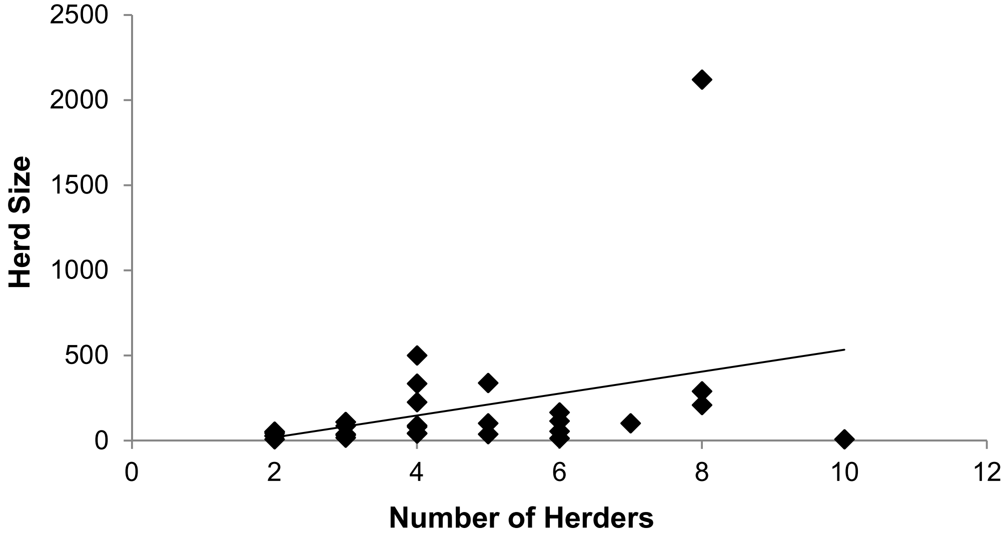


Figure 5.

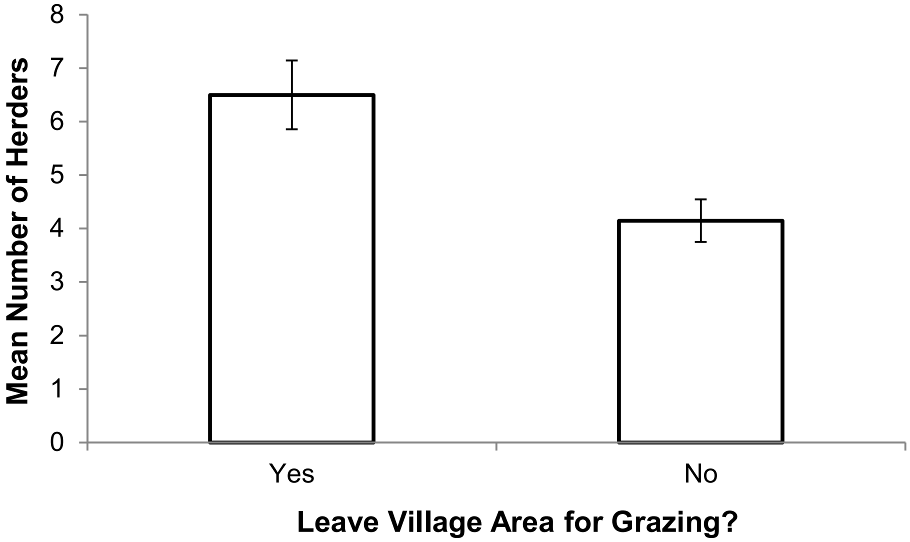


Figure 6.

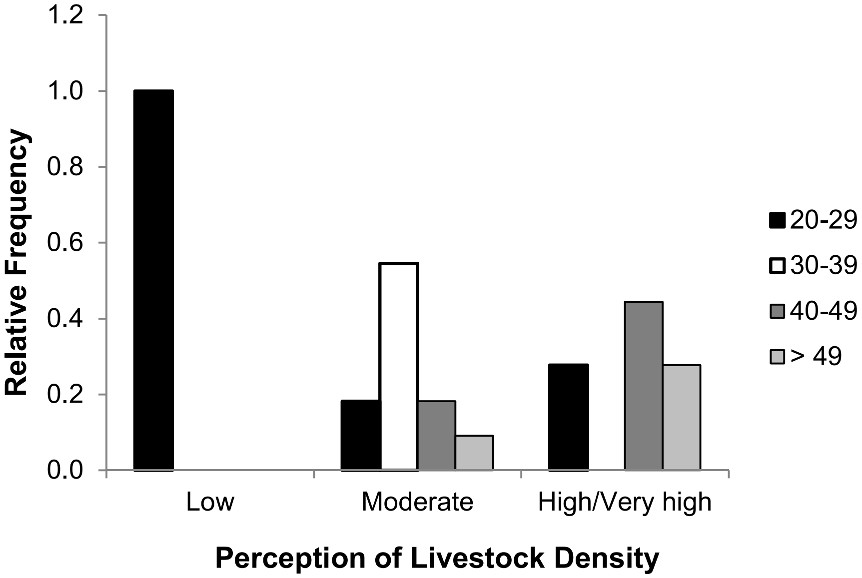


Figure 7.

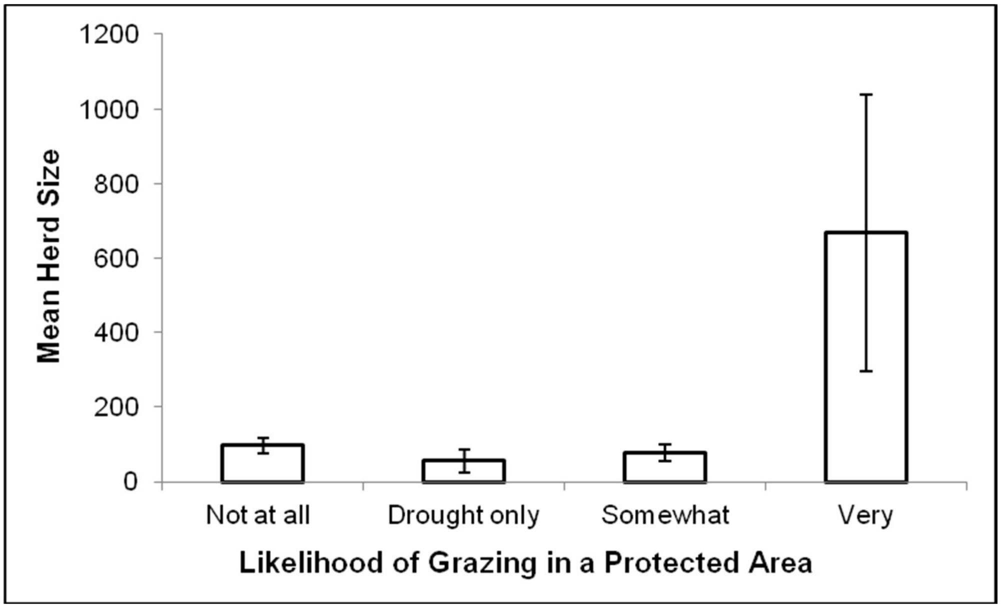
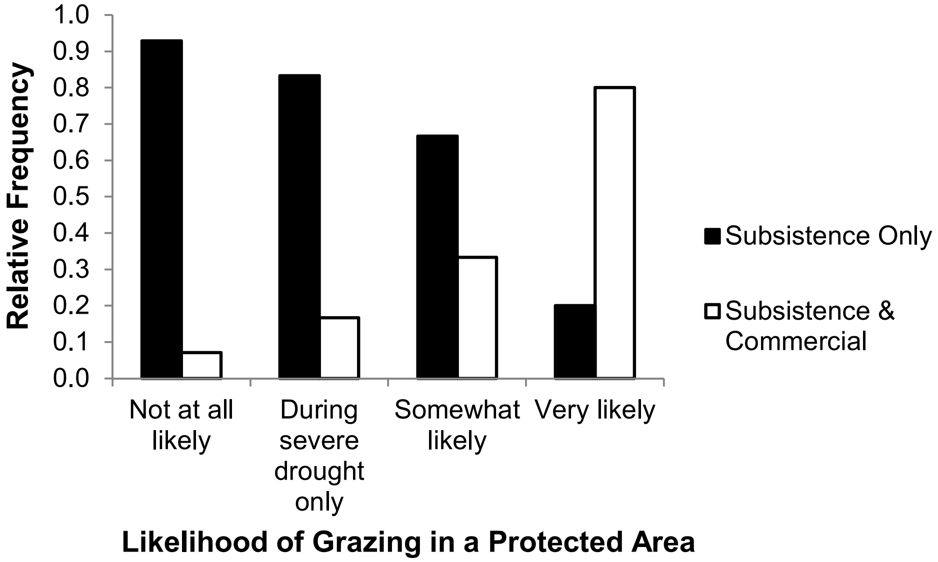


Figure 8.



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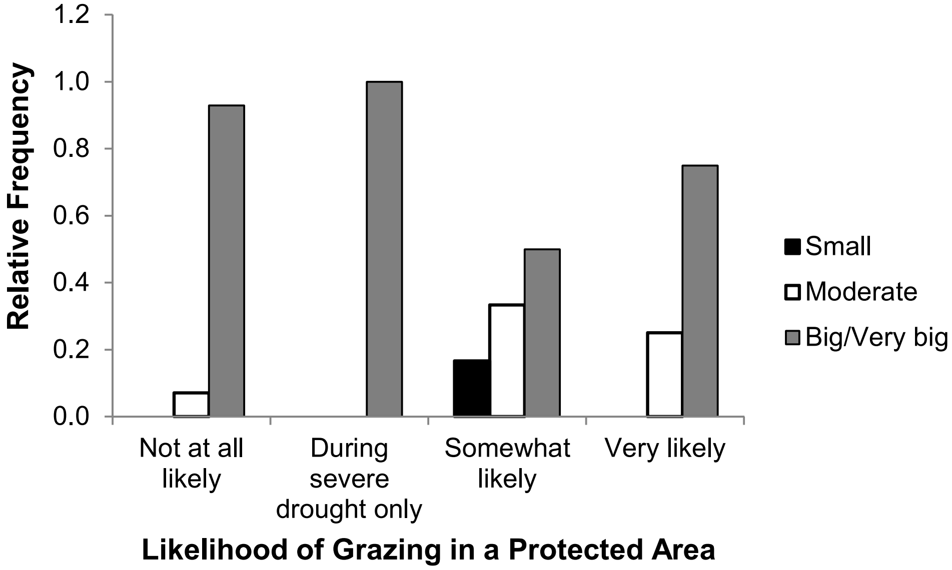
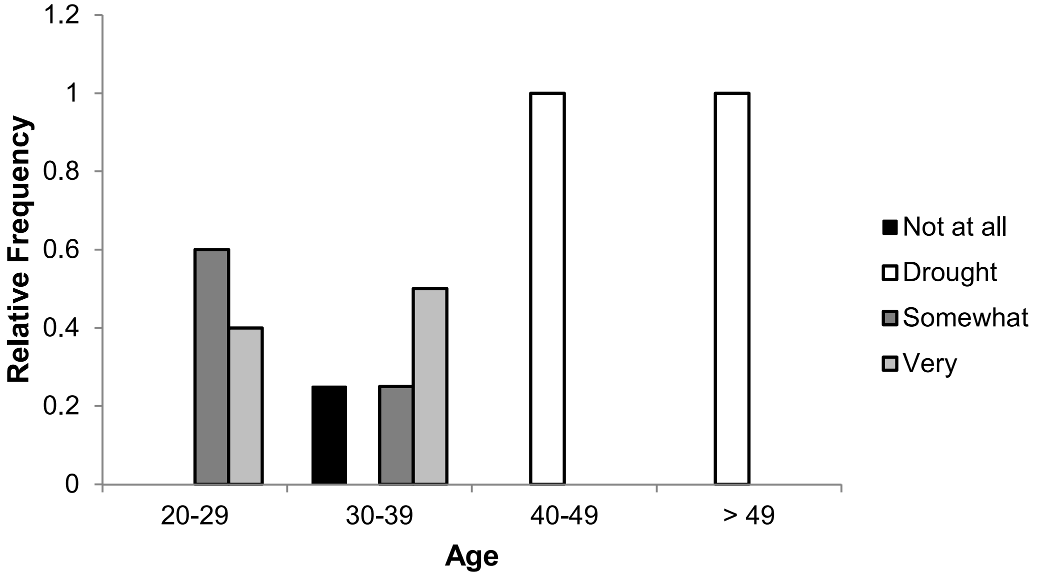


Figure 10.


1.2
1
0.8
0.6
0.4
0.2
0
Relative Frequency
20-29
30-39
40-49
> 49
Age
■ Not at all
□ Drought
■ Somewhat
■ Very

CHAPTER 4

Effects of grazing on grassland soil carbon: a global review

ABSTRACT

Soils of grasslands represent a large potential reservoir for storing CO_2, but this potential likely depends on how grasslands are managed for large mammal grazing. Previous studies found both strong positive and negative grazing effects on soil organic carbon (SOC) but explanations for this variation are poorly developed. Expanding on previous reviews, we performed a multi-factorial meta-analysis of grazer effects on SOC density on 47 independent experimental contrasts from 17 studies. We explicitly tested hypotheses that grazer effects would shift from negative to positive with decreasing precipitation, increasing fineness of soil texture, transition from dominant grass species with C_3 to C_4 photosynthesis and decreasing grazing intensity, after controlling for study duration and sampling depth. The six variables of soil texture, precipitation, grass type, grazing intensity, study duration and sampling depth explained 85% of a large variation ($\pm$ 150 $g{\cdot}m^{-2}{\cdot}yr^{-1}$) in grazing effects, and the best model included significant interactions between precipitation and soil texture ($p= 0.002$), grass type and grazing intensity ($p= 0.012$), and study duration and soil sampling depth ($p= 0.020$). Specifically, an increase in mean annual precipitation of 600mm resulted in a 24% *decrease* in grazer effect size on finer-textured soils, while on sandy soils the same increase in precipitation produced a 22% *increase* in grazer effect on SOC. Increasing grazing intensity increased SOC by 6-7% on C_4-dominated and C_4-C_3 mixed grasslands but decreased SOC by an average 18% in C_3-

dominated grasslands. We discovered these patterns despite a lack of studies in natural, wildlife-dominated ecosystems and tropical grasslands. Our results, which suggest a future focus on why C_3 versus C_4-dominated grasslands differ so strongly in their response of SOC to grazing, show that grazer effects on SOC are highly context-specific and imply that grazers in different regions might be managed differently to help mitigate greenhouse gas emissions.

INTRODUCTION

With the historically recent rise in atmospheric carbon dioxide, it has become increasingly necessary to understand the global carbon cycle and particularly, the role of various potential carbon sinks. Soil is the largest terrestrial reservoir of carbon (Chapin *et al.* 2009), storing more than twice the amount of carbon than the atmosphere (Percival *et al.* 2000) as decomposed plant litter and residue (Cole *et al.* 1993). As grasslands cover approximately 40% of the earth's land surface (LeCain *et al.* 2002; Wang & Fang 2009) and many have suffered recent losses of soil carbon due to intensive livestock or agricultural uses, they may have a high potential to store an appreciable fraction of atmospheric CO_2 as stable C in the soil (Reid *et al.* 2004). Nearly 100% of uncultivated grasslands are grazed by large mammals, and thus, grazing may be a key factor controlling the storage of soil carbon. However, despite considerable research over the past 40 years, much uncertainty exists regarding the effects of grazing on soil carbon.

The major factors that influence soil carbon storage are thought to be related to two types of variables: environmental, including mean annual precipitation and soil type, and study design or sampling methods, such as study duration and soil sampling depth. Biotic variables, such as grassland species composition and grazing intensity are also likely to modify grazer impacts on soil carbon. However, despite strong hints in recent reviews (Derner & Schuman 2007; Pineiro *et al*. 2010) that grazing has varying effects in different environments, the influence of biotic variables is not well explored.

Previous reviews have found mixed results of grazing effects on soil organic carbon (SOC) (Milchunas & Lauenroth 1993; Derner *et al.* 2006), with studies showing positive (Smoliak *et al.* 1972; Wienhold *et al.* 2001; Reeder & Schuman 2002a), neutral (Nosetto *et al.* 2006; Raiesi & Asadi 2006; Shrestha & Stahl 2008) or negative effects of grazing (Su *et al.* 2005; Pei *et al.* 2008; Zuo *et al.* 2008; Golluscio *et al.* 2009). To further explore the drivers of grazer effects on soil carbon, we gathered existing studies of grazing effects on SOC density to conduct a standard statistical meta-analysis. Meta-analyses offer an important advantage over traditional narrative reviews in that they provide a *quantitative* approach to comparing results between studies (Arnqvist & Wooster 1995). Through the use of a common measure of effect size that represents the results of independent treatment comparisons rather than the responses of independent subjects, meta-analyses allow us to determine the combined magnitude of the effect under study and to properly assess its significance (Arnqvist & Wooster 1995). Meta-analyses have proven to be a powerful statistical tool in ecological reviews, yet our study represents a relatively novel approach to the question of how grazing impacts SOC.

Our focus is on grazer effects on carbon *density* as effects on soil carbon *concentration* may be confounded by grazer effects on soil bulk density. Thus, while much informative research has been done using % C and C concentrations, as we were interested mainly in soil's potential to sequester CO_2, (Smith *et al.* 2008), we thought it important to consider only carbon density in our review. We tested for the influence of six factors on grazer impacts on SOC density. These included some previously tested such as soil type, precipitation, and study duration (Derner & Schuman 2007), but also new factors, including whether dominant grass species use C_3 versus C_4 photosynthesis. More importantly, we explicitly tested for interactions between different factors.

First, we tested hypotheses related to the environmental variables of mean annual precipitation and soil texture type. SOC is generally expected to increase with precipitation because of its association with higher productivity and a greater volume of plant litter inputs, particularly belowground (Cole *et al.* 1993; Derner & Schuman 2007b), which increases C inputs to soil. However, two separate reviews (Derner & Schuman 2007; Pineiro *et al*. 2010) found that, under grazing, soil carbon sequestration was increased only at sites with a mean annual precipitation of 600 mm or less. This pattern is attributed to the greater, more active microbial biomass C and more labile organic matter pools in wetter environments, which may increase C turnover under grazing (Derner & Schuman 2007a). The difference in C storage between semi-arid and mesic environments may also be the result of semi-arid areas having lower initial SOC pools, greater root C to soil C ratios, and a grazing-induced compositional shift of plant community to greater C_4 dominance (Derner *et al*. 2006), which may trigger a greater transfer of fixed carbon belowground to roots (Derner & Schuman 2007). In contrast, a different set of studies, mostly from central Asia, found negative effects of grazing on SOC at sites with less than 600 mm mean annual precipitation. In several of these studies (Su *et al.* 2005; Pei *et al.* 2008; Zuo *et al.* 2008; Golluscio *et al.* 2009), this effect appears to be related to increased erosion due to a decrease in vegetation cover associated with continuous, heavy grazing

(Pei *et al.* 2008). Erosion can amplify the negative effects of heavy grazing on leaf area and carbon inputs, as was found in several studies included in our analysis (Li *et al*. 2008; Steffen *et al*. 2008) that featured sparse vegetation cover and/or coarse, sandy soils which are less resistant to wind and rainfall than are finer-textured soils.

Finer soil texture may also potentially strengthen grazer effects on SOC because soils with higher clay content are believed to form tight aggregates that protect SOC from microbes (Feller & Beare 1997; Percival *et al.* 2000; Bronick & Lal 2005) and many studies have found SOC to be correlated with clay content (Arrouays *et al.* 1995; Alvarez & Lavado 1998). Greater precipitation and finer soil texture may thus amplify the magnitude of grazer effects, either positive or negative, rather than shift the direction of effects (Milchunas & Lauenroth 1993).

We also tested hypotheses related to the influence of two biotic variables: grazing intensity and dominant grass species composition. Higher grazing intensity is generally thought to decrease soil carbon by potentially reducing CO_2 fixation from the loss of photosynthetic tissue and reduction in belowground C inputs through lower root production and higher root litter turnover (Gao *et al.* 2008; Klumpp *et al.* 2009). However, grazing-induced changes in allocation of carbon belowground and alteration of root C:N is associated with positive effects of grazing on SOC (Bardgett *et al.* 1998; Reeder & Schuman 2002a). These different responses may in part be due to the dominant grass species, as grazers often increase carbon storage on C_4-dominated grasslands (Wienhold *et al.* 2001, Derner *et al.* 2006, Sanjari *et al.* 2008), but decrease SOC on C_3-dominated grasslands (Potter *et al.* 2001; Li *et al.* 2008; Steffens *et al.* 2008). We expected that grazing intensity might interact with dominant grass species to yield a pattern of positive effects of higher grazing intensity on SOC in C_4 grasslands and negative effects of increasing grazing intensity in C_3-dominated grasslands.

As a control for differences in the sampling design and longevity of experiments, we tested two hypotheses that grazing impacts on soil C would be greater (positive or negative) in longer studies and/or those that sampled only shallow (< 20 cm) depths. We expected that longer studies would have more time for differences in C sequestration to accumulate and would thus show a greater effect. Also, as grazing-induced changes in organic matter may be more likely to occur in the top soil layers, and would thus be diluted by sampling C deeper in the soil profile, we expected a greater effect of grazing in those studies that sampled only at shallower depths.

We considered the influence of these six factors (precipitation, soil texture, grass species composition, grazing intensity, study duration, and soil sampling depth) on grazing impacts on soil C in an ANCOVA analysis that allowed us to determine for the first time the potential separate and interactive influences of biotic and study design variables on grazing effects on SOC, once differences in environmental variables were statistically controlled. This meta-analysis thus provides a potentially more rigorous view of grazing effects on SOC and possible resolution of the disparate experimental results across studies thus far.

METHODS

In an attempt to find virtually every paper that looked at the effect of grazing on soil carbon storage, we conducted a comprehensive search of the ISI Web of Knowledge [v.4.6] - Web of Science® database with the keywords: soil carbon and grazing; soil organic carbon and grazing; soil carbon storage and grazing; carbon sequestration and grazing; grazing intensity and carbon; and livestock grazing and soil carbon. To find additional papers, we checked all references of papers revealed in the database search. We made every attempt to find studies from all continents in order to examine effects across large precipitation gradients. These searches resulted in over 230 papers that studied soil carbon dynamics under different land uses. We narrowed down our sample to 17 studies by including only those studies that compared a grazed sample plot to an ungrazed plot and reported grazer effects on soil carbon density (mass per unit area), or % C together with bulk density, from which we could calculate carbon density, and by including only the most recent results from any ongoing long-term experiments. Unfortunately, many studies reported only % C or C concentrations in g kg^{-1}. Because effects of grazers on soil bulk density can cancel or even reverse effects on C concentration, effects on C concentration may not accurately predict effects on carbon density. These studies were thus excluded from our analysis.

From these 17 studies, we then selected all possible independent pairwise contrasts by first accounting for different sites within a study that differed in one or more of our explanatory variables (such as dominant grass type or soil type) and then accounting for different grazing intensities (light, moderate, or heavy) to a paired ungrazed control within each site. Values of explanatory variables were often averages for each site as studies did not typically provide data for each replicate. This resulted in 47 independent contrasts that compared soil carbon among replicate ungrazed plots to paired grazed plots and in which plot pairs differed in soil type, precipitation, or grazing intensity. For example, a study may have had three different grazing treatments (*i.e.* low, moderate, and high grazing intensity) being monitored on two sites with different soil texture types (*i.e*. coarse, sandy soil and fine, clayey soil) (Potter *et al.* 2001). Provided the study met all other criteria and included ungrazed controls to match each grazing intensity/soil combination, this study would yield six independent contrasts, one for each combination of soil type and grazing intensity. Most of the 17 studies yielded multiple independent contrasts because of within-site variation in grazing intensity and soils, although a few contained sites that also differed in other variables such as mean annual precipitation, dominant grass species type, or study duration.

Our goal was to explain the possible influences of three types of variables, i) environmental, ii) biotic, and iii) study design and sampling methods, on the impact of grazers on soil C. For environmental factors, we considered mean annual precipitation and soil type. Mean annual precipitation values were either reported explicitly within the study or were determined using study location. Soil type was based on soil texture and determined either from authors' reported soil classifications or by using a Soil Textural Class triangle (USDA Natural Resources Conservation Service 1938) and reported percentages of sand, silt, and clay. Soil types were then assigned into one of six 'soil type' classes that fell along a continuum ranging from coarse, sandy soils (1) to fine-textured, clay soils (6). Classes 1-3 had $< 35\%$ clay and $> 30\%$ sand with decreasing sand and/or increasing clay proportions as you move further along the continuum into classes 4, 5, & 6. While other soil characteristics, such as cation exchange capacity, total nitrogen, and pH, may influence soil carbon, these were not reported consistently across studies and therefore could not be evaluated. Next, we included the biotic variables grass type and grazing intensity. Grass type refers to the dominant type of grasses in the community and was determined to be either C_3, C_4, or mixed C_3-C_4 depending on the authors' classification or our classification based on the reported dominant species of the site. Due to a large discrepancy in both the grazing animals used (*i.e.* cattle, goats, sheep) and the units measured (dry sheep equivalent/ha, ha/steer, AUM/ha, etc.), grazing intensity was based on the authors' qualitative classification as light, moderate, or heavy. In a few cases, when a qualitative grazing level was not given, we classified a contrast between grazed and un-grazed conditions based on the authors' description of a site and quantitative information provided on stocking rates relative to precipitation. Finally, for the effects of study design and sampling, we examined both the duration of the treatment and depth of the sampled profile. Rather than treat sampling depth as a continuous variable, we used three depth classes of 0 - 15 cm, 16 - 40 cm, and $>$ 40 cm to avoid biases from a greater preponderance of studies with shallow ($<$ 15 cm) sampling depths. We did not include "study" as a treatment as other variables such as precipitation, soil type, grass type, and study duration together explained much of the variation among studies.

Next, we calculated the effect size of grazing. To do this, we used the standard log response ratio, which entailed taking the natural log of the total C in the grazed site divided by the total C in the ungrazed site (Effect size = $\ln (C_{\text{grazed}} / C_{\text{ungrazed}})$ (Gurevitch 2001). Effect size was used as the dependent variable in our univariate ANCOVA analysis.

With IBM SPSS Statistical Software (SAS 2009), we tested univariate relationships between effect size and each of the six variables using linear regression. We tested for but did not find a correlation between our two quantitative variables (mean annual precipitation and study duration, r = -0.15). We also tested for heteroscedasticity in the relationship between precipitation and effect size, which could be used to infer whether precipitation amplified grazer effect size, by using the Goldfeld-Quandt test (Goldfeld &

Quandt 1965), a version of variance comparison F-tests adapted for linear regression. As we were primarily interested in relationships within each level of the model (environmental, biotic, and design/sampling), we limited interactions to only those between variables at each level. In addition, we were unable to test some interactions across levels due to the lack of representation of grazing effects across the range of values or levels in both independent variables. For example, we were unable to test the interaction between grass type and precipitation because mixed grass types only occurred at a narrow range of annual precipitation (400-600 mm/yr). Mixed grass sites were similarly poorly represented across the range of soil types. Therefore, interactions tested in our analysis included precipitation x soil type, grass type x grazing intensity, and sampling depth x duration. Significant main effects were reported but not interpreted if interaction terms were significant.

We started our ANCOVA analysis with a full hierarchical model (Table 1) that included all of our six variables (soil type, grass type, grazing intensity, and sampled depth as fixed variables and mean annual precipitation and study duration as covariates) and the three interaction terms (precipitation x soil type, grass type x grazing intensity, depth x duration) simultaneously. We then proceeded to test a set of 17 additional candidate models (Supplemental Information S5) based on relationships between the different groups of factors (environmental, biotic, and study design). Next, we used Akaike's Information Criterion with small-sample bias adjustment (AIC_C) and respective AIC weights (Supplemental Information S6) to narrow these down to a smaller set of best models (Table 2). The family of four best models was chosen based on the lowest AIC_C scores and the highest AIC weights and included models that all had AIC weights bigger by a magnitude of 1×10^2 or more than the remaining 14 models in the candidate set (Table 2). From this family of best models we then identified a single best model with an AIC weight at least twenty times as big as the others (Tables 2, 3).

RESULTS

Experiment-long cumulative changes in SOC due to grazing varied considerably from a minimum of -1.6 to a maximum 1.8 kg m^{-2}, corresponding to a range of maximum effect sizes from -0.33 to 0.38 and encompassing studies with an average duration of 31.6 years ($R^2 = 0.76$, df= 2,46, $P < 0.001$). We also calculated amounts of carbon stored annually by dividing cumulative changes by study duration and found maximum gain and loss both were approximately 150 g m^{-2}, again reflecting the same range in effect sizes from -0.33 to 0.38. In this case, effect size accounts for nearly 60% ($R^2 = 0.59$, df = 2, 46, P = 0.003) of the variation in annual change in C.

Most variables in our review were represented by a wide range of values across the different study sites. Mean annual precipitation ranged from 134-932 mm. Soil type ranged from coarse, sandy soils to silt loams to mostly clay soils. Grass type was classified as either a community dominated by C_3 grasses, C_4 grasses, or a mixture of both. Grazing intensity ranged from none in the ungrazed controls to light, moderate, or heavy in the grazed treatments. Duration of treatment ranged from 5-130 years. Depth of the soil profile sampled ranged from 4-200 cm. Despite a wide range in all variables, we found that all studies came from either temperate or subtropical regions, with none in tropical grasslands. Additionally, all studies included in this analysis measured only effects of livestock grazers, rather than native herbivores, on soil carbon storage.

Our full model, with effect size as the dependent variable, started with all nine (6 independent and 3 interaction terms) variables and gave us an adjusted R^2 of 0.695 and an AIC_C of -239.82 (Table 1). Significant variables included mean annual precipitation, grass type, depth, and interactions between precipitation and soil type, grass type and grazing intensity, and depth and duration. Using the 18 candidate models (see Supplemental Information S5 for full description and results), we calculated AIC_C and AIC weights (Supplemental Information S6) in order to identify a set of 4 best models that best explained variability in effect size (Table 2). Included in this set were our full model, a model with only interactions from each level, a model with environmental variables plus biotic (grass x grazing intensity) and design (depth x duration) interactions, as well as our hypothesized best model which included environmental variables, biotic and design interactions plus grass type and depth main effects. The last model, comprised of mean annual precipitation, soil type, grass type, depth, and precipitation x soil type, grass type x grazing intensity, and depth x duration interactions did indeed turn out to be our best model with the lowest AIC_C (-246.14) and the highest AIC weight (0.897). This best model suggests that all six of the factors we examined had significant influences on grazer impacts on SOC, but their manner of influence was largely different than what we hypothesized.

We found no significant univariate relationship between grazer effect on SOC and either precipitation or soil texture. We also found no significant heteroscedasticity between grazer effect and precipitation (Goldfeld- Quandt test: $F = 0.424$, $df = 1, 31$, $P > 0.5$) that would imply that increased precipitation would amplify either positive or negative effects. Rather, soil type and precipitation exhibited a strong interaction in their influence on grazer effects (Table 3, Fig. 1).

We also found a significant interaction between grazing intensity and grass type (Table 3). Specifically, higher grazing intensity was associated with increased SOC in grasslands dominated by C_4 grasses but with lower SOC in grasslands dominated by C_3 grasses (Fig. 2). For mixed grass (C_3 and C_4 grasses co-dominant) sites, which had a more limited sample size, the trend was somewhat less clear, with grazing having a positive effect at both light and heavy grazing intensities and a negative effect at moderate intensities (Fig. 2).

Finally, we discovered a significant interaction between study duration and sampling depth. This interaction showed that in short-term studies, sampling to deeper depths ($>$ 40 cm) tended to result in positive effects of grazing, while sampling to intermediate (15-40 cm) depths produced more negative effects (Fig. 3). Over the longer term, there was little to no effect of sampling depth, as mean effect sizes approached zero for all depth classes (Fig. 3).

DISCUSSION

Compared to other meta-analyses, ours features a relatively small number of studies ($N = 17$) and independent contrasts ($N = 47$), and we were limited to considering only interactions among factors with a wide range of values across sites. Our review also reflects the absence of studies from tropical grasslands and savannas. Additionally, we were unable to evaluate several other potentially important factors, such as fire frequency, soil pH, temperature, type of grazing management (rotational vs. continuous), and wild vs. domestic grazers, etc., because they were not measured in most of the studies we surveyed. Therefore, considerable knowledge gaps about the effects of grazing on SOC still exist and suggest major areas of further research. However, despite these limitations, our analysis did reveal several interesting and informative patterns that reflect the importance of considering the environmental and biotic context of grazing in management decisions designed to help mitigate greenhouse gases and store soil carbon. We discuss these patterns in detail below.

Environmental Influences

We expected that environmental variables would explain the majority of variation in grazer effects on SOC and in fact, precipitation and soil type and especially their interaction together explained a large proportion of the variation (partial Eta-squared = .989) of grazer effect size in our best model (Table 3). The significant interaction reflected that on soils with higher clay content (soil types 4, 5 & 6), grazing has less positive or more strongly negative effects on SOC at higher precipitation (Fig. 1). The opposite trend was found for coarser soils with a high percentage of sand and lower clay content (soil types 1, 2, & 3). For these soils, there is a positive relationship between precipitation and effect size, with grazers having a more positive effect at higher precipitation (Fig. 1). This surprising outcome indicates that the influence of precipitation may depend on soil texture, highlighting likely an important interplay between soil texture, moisture, and the magnitude and fate of belowground C inputs that is considerably more complex than previously suggested (Derner & Schuman 2007b; Pineiro *et al.* 2010).

A few possible mechanisms of how soils and precipitation might interact to affect grazing effects on SOC sequestration have been suggested, but otherwise, such interactions remain poorly explored (Ruess & Seagle 1994; Pineiro *et al.* 2010). Soils of different texture may harbor different microbial C and N (Paustian *et al.* 1992; Zak *et al.* 1994; Knops

& Tilman 2000) and thus impose different demands for C inputs modified by grazing. For example, the positive influence of greater clay content on SOC accumulation may only occur at sites with low precipitation, as decreased microbial activity associated with drier soils may reduce demand for C and amplify the stimulation of belowground production and formation of soil aggregates associated with grazing (Franzluebbers *et al.* 2000; Dominy & Haynes 2002). Possibly, at higher precipitation, finer-textured soils may become waterlogged more frequently and thereby inhibit root growth and thus allocation of C belowground. Compaction of soils by herbivores may further compound this effect (Proffitt *et al.* 1993; Sigua & Coleman 2010). If so, then grazer effects on SOC might become more negative on finer-textured soils. On sandy soils with low precipitation, grazing may result in SOC loss as it more markedly reduces vegetation cover and increases bare ground, thereby accelerating soil drying and erosion (Su *et al*. 2005, Li *et al*. 2008, Pei *et al*. 2008, Steffens *et al*. 2008) and potentially even further coarsening the soil and reducing its capacity to hold SOC (Golluscio *et al.* 2009). These amplifying effects of erosion were in fact posited as a potential mechanism for negative effects of grazing on C in several studies (Li *et al*. 2008, Steffens *et al*. 2008) and may have accounted for some of our most extreme negative effects. Influence of soil texture may also vary with differing soil mineralogy as different minerals have contrasting binding affinities with carbon. However, as most studies did not report mineralogy, we could not analyze it. The interactive effects of precipitation and soils on grazer effects on SOC may also be driven by grassland species composition associated with different precipitation levels. For example, in the North American Great Plains, decreasing precipitation is associated generally with an increase in the relative abundance of C_4 vs. C_3 grasses and an overall increase in grazing intensity

(Naeth *et al.* 1991; Derner *et al.* 2006). As we show below, grassland species composition may strongly affect grazer impacts of SOC.

Biotic Influences

Virtually no studies have explicitly suggested that grassland species composition should strongly influence grazer effects on SOC or that it should modulate the influence of grazing intensity. However, with the second highest proportion of variance (partial Eta-squared = 0.758) after environmental variables (partial Eta-squared = 0.989) (Table 3), both grass type and grazing intensity appear to be important, and perhaps more so, than previously realized. Our analysis suggests that these two factors may interact as key biotic drivers of grazer effects on SOC independently of effects from precipitation and soil texture. This interaction shows that, at sites dominated by C_3 grasses, grazing had a positive effect on SOC only at light grazing intensities and this effect became negative at moderate to heavy intensities. In contrast, for grasslands dominated by C_4 grasses, grazer effects shifted from slightly negative at light grazing intensities to positive for moderate and heavy intensities.

C_4 grasses and their response to grazing may be responsible for most cases where positive effects of grazers on SOC have been measured. Several studies implicate the stimulation of fine, shallow roots by grazing in C_4 species, such as *Bouteloua gracilis*, in grazer-induced increases in SOC (Frank *et al.* 1995; Derner *et al.* 2006). Such increase in belowground C allocation may provide C_4 grasses with a competitive advantage, and the difference in SOC in a few studies may be a reflection of the relative dominance of C_4 grasses under grazed conditions and C_3 grasses in the absence of grazing. Such species shifts may explain the response in SOC to grazing we observed in the studies of mixed-C_3 –

C_4 grass assemblages in our database (Reeder & Schuman 2002b; Reeder *et al.* 2004) (Fig. 2). Ungrazed and moderately grazed plots may have been typically dominated by C_3 grasses such as *Pascopyrum smithii*, which may have responded in the ways mentioned above that led to a significant decline in SOC (Reeder & Schuman 2002b). At higher grazing intensity, C_4 species, such as *B. gracilis,* may have largely replaced C_3 species, and typical C_4 grass responses to grazing significantly stimulated SOC (Frank *et al.* 1995; Reeder & Schuman 2002b; Derner *et al.* 2006). C_4 grasses may also yield more SOC than C_3 grasses because of higher root-to-shoot ratios and greater transfer of photosynthate belowground (Reeder *et al.* 2004), or because of greater root density and turnover and possibly, higher rates of root exudate (Frank *et al.* 1995).

Differences in mycorrhizal association with C_3 and C_4 grasses may also help explain the importance of species composition in SOC response to grazing. Mycorrhizae have been shown to infect the roots of C_4 grass much more than C_3 grasses (Wilson & Hartnett 1998) and grazing can stimulate the production of mycorrhizal hyphae (Eom *et al.* 2001; Johnson *et al.* 2006; Medina-Roldan *et al.* 2008). Mycorrhizae excrete a substance called glomalin which acts like a glue that binds soil into aggregates (Treseder & Turner 2007). Thus, increased mycorrhizal production and associated glomalin excretion could be significant in allowing soil under C_4 grasses, as opposed to C_3 grasses, to store carbon under heavier grazing (Franzluebbers *et al.* 2000; Treseder & Turner 2007; Klumpp *et al.* 2009; Wilson *et al.* 2009).

Yet another mechanism that might explain differences in C_3 vs. C_4 grassland SOC response to grazing is an interaction between fire and grazing. C_4 grasses appear to burn more frequently and putatively have evolved high flammability to promote fire (Clark *et al.*

2001; Keeley & Rundel 2005). While much of aboveground biomass consumed by herbivores may be respired as CO_2, up to 50% may be deposited on the ground surface as dung. Under some conditions, a considerable fraction of dung can be incorporated into soil organic matter (Bol *et al.* 2000; Dungait *et al.* 2009). Grazers may therefore effectively re-direct carbon from a source of aboveground loss (combusted biomass) to a source of belowground sequestration (soil organic matter), and this effect would be stronger where fire frequencies are higher. Because of the greater propensity for C_4 grasslands to burn, this possible re-direction of carbon by grazing may make it more likely that grazing, particularly heavy grazing, increases SOC in C_4-dominated grasslands. To our knowledge, the consequences of fire-grazer-soil interactions for SOC sequestration in grasslands have not yet been explored.

Higher grazing intensity is generally expected to lead to greater SOC loss because greater removal of photosynthetic tissue and subsequent respiration of assimilated C by grazers reduces potential C inputs to soil organic matter (Derner & Schuman 2007b; Gao *et al.* 2008; Klumpp *et al.* 2009). A recent mesocosm experiment done in France (Klumpp *et al.* 2009) showed that by shifting disturbance (*i.e.* grazing and/or clipping) frequency of C_3-dominated grass turfs from a previous long-term (14-year) low disturbance regime to high frequency disturbance led to a cascading set of effects that included a reduction in root biomass, a decline in soil fungi, and an increase in gram (+) bacteria that ultimately hastened decomposition of old (> 6 months) particulate organic C. Greater decomposition released plant available nitrogen and further stimulated microbial decomposition and lowered SOC (Klumpp *et al.* 2009). Our review supports these findings for the C_3-dominated grasslands of Inner Mongolia and Patagonia (e.g., Steffens *et al.* 2008, Golluscio *et al.* 2009), but clearly shows an opposite trend in both mixed C_3-C_4 and C_4-dominated grasslands where increasing grazing intensity was associated with more positive effects of grazing on SOC.

Influences of Study Design

In our analysis, we expected that longer studies with shallow sampling would detect a larger grazer effect. SOC accumulation typically takes years to detect, particularly in sparsely replicated field experiments, because soil annual changes are small relative to standing stocks of SOC and SOC can vary considerably over distances of a few meters (Paustian *et al.* 1992; Conant *et al.* 2001). Consequently, a large percentage change in soil carbon is often required to measure significant differences in SOC density. Shorter studies (< 20 years' duration) might be less likely to detect differences in SOC between treatments. Shallower sampling might more readily detect changes in SOC as changes in C inputs more likely affect shallow soil layers where the majority of root production occurs (Medina-Roldan *et al.* 2008). However, we failed to detect a univariate association between effect size and either duration or sampling depth and together design variables accounted for the lowest proportion of variance (partial Eta-squared = 0.588) in our model (Table 3). In the studies we reviewed, most exclosures had been in place 10-25 years, and measured differences in SOC between treatments may not have been as sensitive to differences in duration as other environmental and biotic factors that differed between sites. Instead an interaction between study duration and sampling depth showed positive effects of grazing in short-term studies that sampled to deeper depths (> 40 cm) but negative effects in those that sampled to intermediate (15-40 cm) depths (Fig. 3). Perhaps sampling to intermediate depths is more sensitive to declines in root biomass at depth with grazing, which even for C_4 grasses declines at deeper depths (Nippert *et al.* 2012), whereas sampling to deeper depths may pick up carbon sequestered in the finer-textured soil that occurs at greater depth (Jobbagy & Jackson 2000; Pineiro *et al.* 2009). These hypotheses are speculative as data are generally lacking on the simultaneous effects of grazing on rooting depth and soil carbon.

On the other hand, for longer-term studies, sampling depth had little to no effect. Longer-term studies may not show any effect of depth possibly because the grazed and ungrazed conditions are at or near their respective equilibria throughout the soil column after 25-40 years (Conant *et al.* 2001). Given that these design influences account for the residuals after incorporating all the other major factors, these results are unlikely to result from hidden correlations between study duration, sampling depth and soil type, such as if fine textured soils tended to be sampled to shallower depths because of the difficulty in coring tight soils.

Implications for Global Change

In our analysis of a global range of studies, we found that grazing has significant large, but highly variable, effects on SOC density that depend on the context of climate, soils, grass type, and grazing intensity. First, grazer effects on SOC, whether positive or negative, are potentially large, with cumulative changes of up to 1.6 kg/m^2 (16 tons/ha) over 10-30 years and annual changes as large as $\pm$ 150 g/m^2 (1.5 $tons{\cdot}ha^{-1}{\cdot}yr^{-1}$). The roughly equal distribution of positive and negative effects suggests that, as noted in previous studies, the sign of the effect of grazers on SOC is highly context-dependent. Secondly, interactions between the different levels of factors (soil type and precipitation, dominant grass type and grazing intensity, and study duration and sampling depth) were much stronger than relationships between grazer effects and any single factor.

Our results have some key implications for management of grazing to sustain soil organic matter and to generate C offsets for carbon markets that seek to help reduce greenhouse gases (Henry *et al.* 2005; Lal *et al.* 2007; Smith *et al.* 2008). For example, reducing grazing might be counterproductive on C_4 grasslands but may, in fact, be necessary to avoid chronic SOC loss in C_3 grasslands. Currently, there may be major regions of the globe where grazing is already sequestering carbon, such as in tropical or temperate grasslands dominated by C_4 grasses (Holdo *et al.* 2009). There may also be large areas degraded by past overgrazing, such as in many of the world's C_3- dominated grasslands, where decreasing grazing intensity could lead to C sequestration (Conant *et al.* 2001). Such actions could allow grazing to significantly contribute to mitigating greenhouse gases and help increase the impact of soils as global carbon sinks (Lal *et al.* 2007). However, climate may also influence appropriate prescriptions for management, as intense grazing may not be appropriate at some coarse soil sites, regardless of dominant grass type. Furthermore, it is important to consider how grazing effects on soil C may be impacted by expected changes in climate such as an increased frequency of drought and heat wave events that might turn grasslands into C sources (Ciais *et al.* 2005). Other impacts, such as the combination of long-term drought with high atmospheric CO_2 concentration could decrease soil microbial biomass and promote shifts in functional microbial types, in turn leading to further changes in biogeochemical cycles and C sequestration (Barnard *et al.* 2006, Pinay *et al.* 2007, Bloor & Bardgett 2012). Finally, it is also necessary to consider impacts of grazing management on other biogenic greenhouse gases like N_2O and CH_4, as increased emissions of these gases could potentially offset substantial C sequestration (Conant *et al.* 2005) and thereby limit the utility of management actions.

Our results also provide insight on how grazing might influence grasslands' vulnerability to climate change. For example, moderate grazing in tropical grasslands that generates positive soil carbon storage could additionally result in increases in productivity and soil water-holding capacity (Belknap *et al.* 2005; Teague *et al.* 2011) that might make grasslands better able to withstand climatic changes. On the other hand, intense grazing in grasslands on dry, sandy soils such as those found in Central Asia, may cause them to become more vulnerable to drought through the cyclical forces of reduced vegetation cover, increased wind erosion, and coarsening of the soil- all factors which might cause grasslands to become a carbon source rather than a sink. In contrast, grazing on finer-textured soils may become more sustainable with a drying climate as our results show positive effects of grazing at arid sites with clay soils (Fig. 2). Finally, a shift to a drier, warmer climate may produce a shift in dominant species composition from C_3 to C_4 grasses in many parts of the world, which may make moderately intense grazing a more suitable land use practice than under current conditions in C_3 grasslands.

Ecologists and land managers should consider this complete context before they can fully understand the potential influence of grazing on soil carbon. Nevertheless our review provides a statistical model that explains considerable (partial Eta-squared = 0.848) variation in grazing effects among and even within sites, despite the relatively small number of available studies and independent contrasts of grazing effects on carbon density. Our results suggest that ecologists still have much to learn about how grazing affects soil carbon because all factors in our analysis, including soil texture, precipitation, grass species composition, grazing intensity, sampling depth, and study duration, interacted in complex ways to determine effects of grazing on SOC density. The patterns we detected contradict many of the current favorite hypotheses about grazing effects on SOC, such as the expected general dependence of positive grazing effects on low rainfall and finer-textured soils.

Another key discovery is that grazing effects on SOC density in tropical grasslands remain virtually unstudied. By virtue of the dominance of C_4 grasses in the tropics, moderate grazing might increase SOC, making tropical grasslands an important global carbon sink (Holdo *et al.* 2009). Because of the potential importance of grasslands in building soil fertility for sustainable development and in reducing greenhouse gases, the role of grazing in affecting SOC in tropical regions would seem to be an important, and fruitful, area of future research.

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Table 1. Results of full univariate ANCOVA model to explain grazing effect on soil organic carbon density ($R^2 = 0.848$, Adjusted $R^2 = 0.695$, $AIC_C = -239.82^a$).

Source	df	Type III Sum of Squares	F	*p*
Corrected Model[b]	23	.911	5.566	.000
Intercept	1	.006	.865	.362
Mean Ann Precip (mm)	1	.039	5.411	.029
Soil Type	4	.067	2.355	.084
Mean Ann Precip (mm) x Soil Type	4	.169	5.929	.002
Grass Type	2	.062	4.380	.024
Grazing Intensity	2	.000	.025	.976
Grass Type x Grazing Intensity	4	.149	5.229	.004
Depth Category (cm)	2	.053	3.730	.040
Duration of Treatment (years)	1	.012	1.662	.210
Depth (cm) x Duration (years)	2	.071	4.986	.016
Error	23	.164		
Total	47	1.089		
Corrected Total	46	1.075		

a= Akaike's Information Criterion (AIC) (Akaike 1985, Burnham & Anderson 1992) with the small-sample bias adjustment ($AIC_C = n * [\ln (SSE / n)] + 2K + [(2K * (K + 1)) / (n - K - 1)]$) (Hurvich & Tsai 1995, Burnham and Anderson 2002); b= "Corrected Model" is composed of variability sources from all 10 parameters in the model, from "Intercept" to "Depth (cm) x Duration (years)". Bold type indicates variables also present in the best model shown in Table 3.

Table 2. Model selection results of the four best models in the meta-analysis, based on Akaike's Information Criterion with small-sample bias adjustment (AIC$_C$) and AIC weights (w_i) (see Supplemental Information S6 for explanation).

Model	K[a]	SSE[b]	AIC$_C$[c]	Δ_i[d]	w_i[e]
P[f], S[g], PxS[h], G[i], GxGI[j], D[k], DxDu[l]	8	0.164	-246.14	0.00	0.897
PxS, GxGI, DxDu	4	0.235	-240.07	6.07	0.043
P, S, PxS, G, GI[m], GxGI, D, Du[n], DxDu	10	0.164	-239.82	6.32	0.038
P, S, PxS, GxGI, DxDu	6	0.217	-238.67	7.47	0.021

In table, a= number of parameters in the model, including intercept; b= sum of squares error in the model; c= Akaike's Information Criterion (AIC) (Akaike 1985, Burnham & Anderson 1992) with the small-sample bias adjustment ($AIC_C = n * [\ln (SSE / n)] + 2K + [(2K * (K + 1)) / (n - K - 1)]$) (Hurvich & Tsai 1995, Burnham and Anderson 2002); d= difference between best model and each model in set, AIC_i - AIC_{min}; e= AIC weight, $w_i = \exp(-0.5 * \Delta_i) / \sum_{r=1}^{R} \exp(-0.5 * \Delta_i)$ (Burnham & Anderson 2002); f= Mean annual precipitation (mm); g= Soil texture type (see Methods for category descriptions); h= an interaction term for precipitation and soil type; i= Dominant grass species type (C_3, C_4, or mixed); j= an interaction term for grass type and grazing intensity (light, moderate, or heavy); k= Sampled soil depth (cm), l= an interaction term for soil depth and study duration (years); m= Grazing intensity; and n= Study duration.

Table 3. Best model to explain grazing effect on soil organic carbon based on AIC_C and AIC weights from a set of 4 best models (R^2= 0.848, Adjusted R^2= 0.695, AIC_C= -246.14[a]).

Source	df	Type III Sum of Squares	F	P
Corrected Model[b]	23	.911	5.566	.000
Intercept	1	.006	.865	.362
Mean Ann Precip (mm)	1	.039	5.411	.029
Soil Type	4	.067	2.355	.084
Mean Ann Precip (mm) x Soil Type	4	.169	5.929	.002
Grass Type	2	.062	4.380	.024
Grass Type x Grazing Intensity	6	.152	3.565	.012
Depth Category (cm)	2	.053	3.730	.040
Depth (cm) x Duration (years)	3	.085	3.996	.020
Error	23	.164		
Total	47	1.089		
Corrected Total	46	1.075		

a= Akaike's Information Criterion (AIC) (Akaike 1985, Burnham & Anderson 1992) with the small-sample bias adjustment ($AIC_C = n * [\ln (SSE / n)] + 2K + [(2K * (K + 1)) / (n - K - 1)]$) (Hurvich & Tsai 1995, Burnham and Anderson 2002); b= "Corrected Model" is composed of variability sources from all 8 parameters in the model, from "Intercept" to "Depth (cm) x Duration (years)".

FIGURE CAPTIONS

Figure 1. Significant regressions of effect size of grazing on SOC associated with mean annual precipitation when presented separately for sandy soil types (indices 1, 2 & 3, solid circles; df = 1, 26, $P = 0.033$, $R^2 = 0.162$) and finer-textured soils (indices 4, 5 & 6, open squares; df = 1, 17, $P = 0.024$, $R^2 = 0.264$).

Figure 2. Mean (± SE) residual effect size of grazing on SOC after accounting for associations with soil type, precipitation and a soil x precipitation interaction for three different categories of grazing intensity (see Methods for definition) and three different types of grass species composition. Contrasts for each grazing intensity level indicate a significant overall interaction between grass species composition and grazing intensity in explaining grazer effects on SOC.

Figure 3. Relationship between residual grazer effect size on SOC after incorporating environmental and biotic variables versus study duration for three different sampling depth classes (see Methods for definition).

Figure 1.

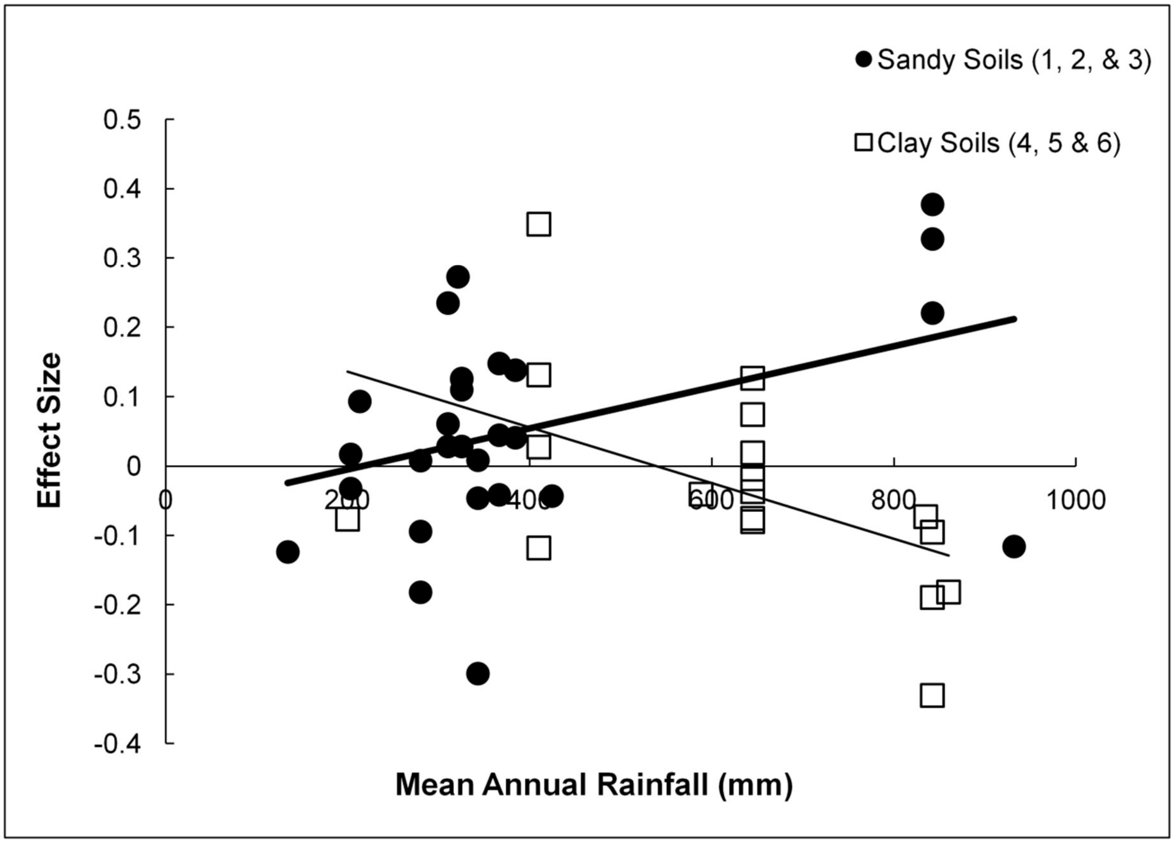

● Sandy Soils (1, 2, & 3)
□ Clay Soils (4, 5 & 6)
Effect Size
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
200
400
600
800
1000
Mean Annual Rainfall (mm)

Figure 2.

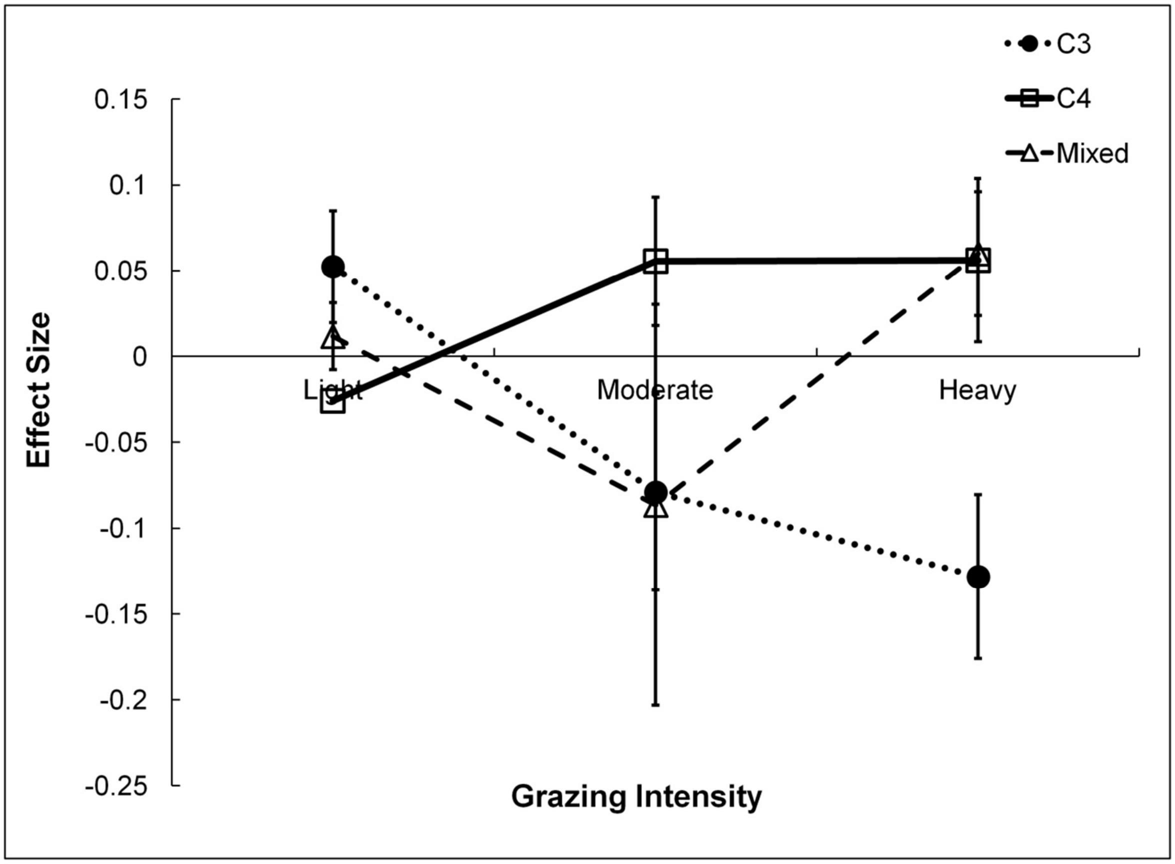
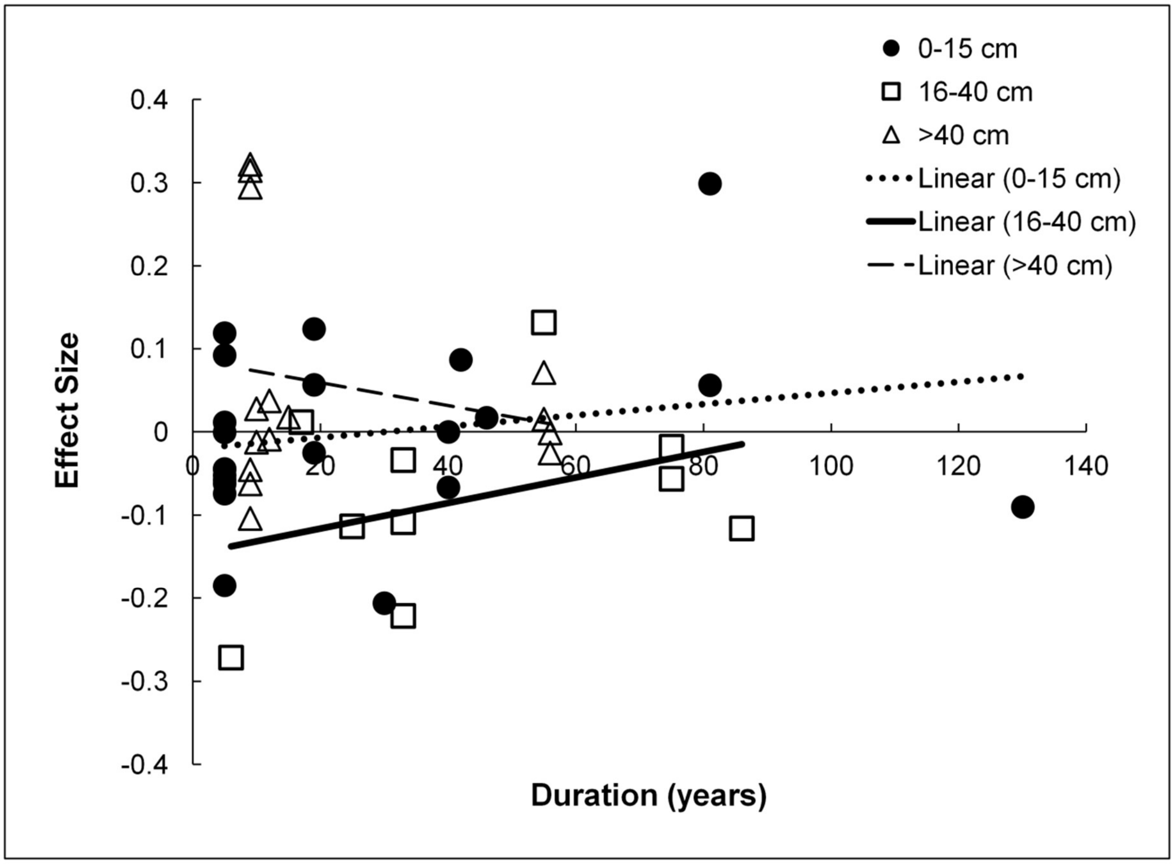

C3
C4
Mixed
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
-0.25
Effect Size
Light
Moderate
Heavy
Grazing Intensity

Figure 3.


● 0-15 cm
□ 16-40 cm
△ >40 cm
Linear (0-15 cm)
Linear (16-40 cm)
Linear (>40 cm)
Effect Size
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
20
40
60
80
100
120
140
Duration (years)

CHAPTER 5.

Synthesis and conclusions: interpreting ecological data in the context of socioeconomic and cultural conditions

"Human institutions- ways of organizing activities- affect the resilience of the environment."

- T. Dietz, E. Ostrom, & P. Stern (*Science*, 2003)

Many issues surround the uncertainty of large herbivore grazing impacts, particularly in human-natural systems that are home to both native wildlife and domestic livestock. Some of these pervasive issues include, but are not limited to, apparent or perceived (Gadd 2005) competition between native and domestic herbivores over resources such as water and forage (Voeten & Prins 1999; Young *et al.* 2005); destruction or degradation of plant and water resources by wildlife or livestock with impacts on their quality (Agouridis *et al.* 2005) and/or quantity (Skarpe 1991; Redfern *et al.* 2005); conflicts over space, including both shared spaces (Prins 1992) and those where livestock are prohibited (Nyahongo *et al.* 2005; Shrestha & Dangol 2006); and lastly, the risk of transmission of disease between groups (Bengis *et al.* 2002; Morgan *et al.* 2006). These issues are frequently further compounded by the other important, but oft-overlooked, group of actors in these systems: humans. Human activities including sedentarization (the settling in one place of a formerly nomadic or transhumant population) (Niamir-Fuller 1999; Galvin 2009; Western *et al.* 2009), the expansion of agricultural activities (Sinclair *et al.* 2008), and the practice of illegal activities, including hunting of native wildlife

(Kaltenborn *et al.* 2005) and grazing in prohibited areas (Nyahongo *et al.* 2005), can further exacerbate pressure on a coupled human-natural grazing system. These issues are not only characteristic of the study region focused on in Chapters 2 & 3 but in similar systems across Africa (Gusset *et al.* 2009; Butt & Turner 2012) and the globe (Mishra 1997; Bader & Finstad 2001; Mishra *et al.* 2001; Madhusudan 2004; Mishra *et al.* 2004; Dong *et al.* 2007; Chhangani *et al.* 2008; Kilpatrick *et al.* 2009), with potential ramifications for plant and soil health as we see in Chapter 4.

This body of work has been an attempt to explore some of the questions regarding impacts of large herbivore grazers on the many interconnected properties that play a role in a grassland ecosystem's function and resiliency. Understanding how herbivores maintain or degrade grassland function and resiliency is critical not only to resolving many of the above issues but also to preserving the many important benefits derived from grasslands, ranging from the vital ecosystem services and the potential economic opportunities they provide to the spectacular biodiversity they support. And while the study of grazer impacts is certainly not a new topic of study, there remain many questions about how and why some impacts are negative, while others affect the system positively. This study has attempted to address one area of this uncertainty by focusing on differences in impacts due to herbivore type, more generally referred to as 'management', as the type of herbivore a system is managed for influences nearly every aspect of management including human interference, restriction or delineation of grazing areas, control of fire, etc. While many studies have covered the impacts of grazing on various aspects of ecosystem function (McNaughton 1976; Bryant *et al.* 1983; Ruess & McNaughton 1987; Seagle *et al.* 1992;

Frank & McNaughton 1993; Milchunas & Lauenroth 1993; Noy-Meir 1993; Vinton *et al.* 1993; Hartnett *et al.* 1996; Hobbs *et al.* 1996; McNaughton *et al.* 1997; Augustine & McNaughton 1998; Oba *et al.* 2000; Hickman *et al.* 2004; Cingolani *et al.* 2005; Hendricks *et al.* 2005; Anderson *et al.* 2006), very few have actually compared these impacts for areas managed for domestic and native herbivores side-by-side in their natural environments.

Chapter 2 addresses this gap with a comparative grazing experiment in an ecosystem that is being managed ‘naturally’ by governmental bodies for wildlife conservation on one side of a border and dominated by individual- and village-organized farms and livestock grazing on the other. This study compares grazer impacts on plant community composition, an important indicator of ecosystem resiliency as it is linked to plant productivity (Tilman *et al.* 1997) and soil carbon (Bagchi & Ritchie 2010). A significant finding from this study reveals that livestock grazing may not always be as negative as it is often touted to be (McNaughton 1993; Painter & Belsky 1993). Rather, results show that while differences in plant composition do exist across management types, once grazing is relaxed, composition across livestock- and wildlife-grazed areas at least *begin* on a path toward greater similarity, indicating that the livestock-grazed system has retained the resiliency to “bounce back” to natural conditions. Therefore, even obvious visual differences in plant height or structure across livestock-grazed and wildlife-grazed grasslands (Figure 1) do not necessarily indicate ecosystem degradation or a reduction in ecosystem resiliency. While the short length of this experiment clearly limits the conclusions to be drawn from this result, it suggests that grazing by livestock (even in confined areas subject to continuous heavy grazing pressure) has not changed the species pool to such a degree that it is resistant to changes following grazing reduction. This provides preliminary evidence that, in this system, livestock grazing has not yet been such a large disturbance to have driven a shift in plant community to an alternate stable state (Schacht 1993; van de Koppel *et al.* 1997; Bestelmeyer *et al.* 2003; Stringham *et al.* 2003).

These results, while in need of further verification over a longer time period, nonetheless have significant implications for management, particularly in human-natural systems such as the Serengeti or other wildlife-rich areas of Africa where livestock and wildlife grazing frequently occur side by side, as they suggest that managing the level of grazing intensity is one way to mitigate livestock impacts. Furthermore, the trend toward convergence of composition in paired livestock-grazed and wildlife-grazed plots managed at similar levels of grazing pressure illustrates that how an area is managed, which includes both the overall grazing intensity and the spatial and temporal *distribution* of grazing pressure (Oesterheld *et al.* 1992; Turner *et al.* 2005), may have more of an effect on the magnitude and direction of grazing impacts than the set of herbivore species you place upon it (Ritchie & Olff 1999; Rook *et al.* 2004) (*i.e*. whether native or domestic). This is significant as it suggests that the (often smaller) suite of domestic grazers (typically some combination of cattle, sheep, goat, & equid) may nevertheless be functionally similar to their native counterparts (Chapter 2) and thus, could be managed in such a way as to mimic the positive impacts of wildlife herbivores, rather than be doomed to a path of irreversible degradation. In fact, a study done by Bagchi and Ritchie (2010) found that directional effects on composition, driven by overlapping selectivity across species for particular functional groups, had more to do with whether animals were free-ranging or herded tightly together in groups. Thus, managing for resiliency may not be merely adjusting how much production is consumed in a given period (grazing intensity), but also managing how animals are moved across the landscape and whether they are free-ranging or tightly herded during grazing activities (Bagchi & Ritchie 2010).

The importance of accounting for grazing management in understanding herbivore impacts was also highlighted in Chapter 4 with the novel finding that the level of grazing intensity that promotes soil carbon storage is dependent on the dominant grass type of the system. Specifically, grazer effects on soil carbon were positive at moderate to high grazing intensities only on grasslands dominated by C_4 grasses, while anything above a light grazing intensity in C_3-dominated grasslands induced SOC loss. Tropical grasslands may exhibit a greater potential for resiliency when it comes to grazing activities than temperate systems due in part to the longer coevolutionary history between plants and large grazers. This finding, related to those from Chapter 2, highlights a mechanism through which grazers can impact ecosystem resiliency, as grazer impacts on plant community composition indirectly affect soil carbon levels, likely through changes in the magnitude of carbon inputs (Bagchi & Ritchie 2010). While previous studies on grazer effects on soil carbon had compared grasslands and rangelands by the amount of annual precipitation that fell on them (Derner & Schuman 2007a) or by the type of soil supporting the vegetation, most had largely ignored the question of whether effects might differ based on whether grasses were predominantly warm-season C_4 grasses or cool-season C_3 grasses. Through a meta-analysis of studies of grazer impacts on soil organic carbon (SOC) conducted at sites all across the world (though studies in some regions were notably lacking), we learned that, even at the global level, the importance of the environmental and management context breaks through. Effects of grazing on SOC storage were driven in large part by the broad environmental conditions they were placed in. The type of soil, the amount of rainfall, the dominant type of grass species and grazing intensity all interacted to determine whether the impact would be negative, causing more carbon lost to the atmosphere, or positive, storing additional carbon in the soil and potentially revealing an opportunity for revenue to be made through the sale of carbon credits. This study illuminates several important factors (soil type, precipitation levels, etc.) for managers or researchers to consider in determining the potential of a particular rangeland or grassland for carbon sequestration and it also provides useful information to managers on how to manage grazing intensity for SOC storage within a given set of environmental conditions. Managing grazing intensity may not only help to maintain ecosystem resiliency, but might also increase carbon sequestration, which could potentially help in mitigating climate change or even generate revenue through carbon credits.

While Chapter 4 addressed the importance of adjusting management via a raising or lowering of grazing intensity, Chapter 3 builds off of the hypothesis regarding the importance of managing the spatial and temporal patterns of grazing and asks what drives these patterns in livestock systems. This question instantly becomes more than just an ecological one as livestock decisions are inevitably made by human managers, each influenced by their personal circumstances and experiences and informed by their own set of opinions and beliefs. This chapter aimed to uncover which among those characteristics and perceptions were important in influencing herd movement decisions, and thus resulting spatial patterns of livestock grazing. Herding mobility among pastoralists typically falls under one of two strategies: ‘sedentary herding’ (Baker & Hoffman 2006), which is characterized by daily movements from a permanent base, often in the direction of a water source (Adriansen & Nielsen 2002) and ‘mobile herding’ (Baker & Hoffman 2006), typified by some degree of transhumance, or moving from place to place using temporary camps. Transhumance is usually driven by the lack of pasture or water nearby or the search for better quality pasture (Adriansen & Nielsen 2002) but often pastoralists and agropastoralists are “constrained by the need to start and end resource collection at a central place” (Coppolillo 2001) (often a permanent home or farm but also possibly an area in proximity to a school or health care facility, etc.) and are therefore unable to practice transhumance. This central-place constraint forces many pastoralists, especially agropastoralists, into the sedentary herding strategy (Baker & Hoffman 2006) and this was true for most respondents in the focal study-villages. This type of herding strategy is more likely to have a negative environmental impact on grassland resources, particularly in arid areas, due to the heavy, localized use of a smaller area (Baker & Hoffman 2006).

Previous studies have noted the heterogeneity that exists within communities in terms of assets, social status, and ethnic origin, all factors which play a role in determining how an individual will choose to go about resource collection as well as how they respond to encroachment by other resource-users (Baker & Hoffman 2006; Bogale & Korf 2009). Therefore, this study collected individual responses in order to capture the individual variation that affects these decisions. However, key patterns and themes did emerge, including: 1) the stress facing livestock owners who are being increasingly confined to a smaller and smaller resource capture area is, in some cases, increasing perceptions of competition; 2) the degree of enforcement of livestock-prohibition policies within protected areas and the associated levels of 'realized risk' facing livestock owners affects how much an adjacent protected area influences herders' livestock movement decisions, particularly regarding the choice to graze illegally; and 3) despite these restrictions on the number of movement *options*, individual movement decisions were nonetheless found to be related to characteristics such as herd size and for what purpose animals are kept. This last finding parallels that from Sieff's (1997) study of the herding strategies of the Datoga pastoralists, also from northern Tanzania, which found that both the number of groups herds are split into and the number of animals looked after by a herder increased with the total number of animals owned by the livestock owner (Sieff 1997).

In a study of the Wasukuma agropastoralists of western Tanzania, Coppolillo (2000) found that the dry season 'herding radius' (*i.e.* the maximum distance travelled from home in a day) was closely correlated with distance to water, indicating that water availability has a strong influence over the distribution of grazing, at least in the dry season. This is also likely the case in Kijereshi (also inhabited by Wasukuma) and Isenye regions, where respondents described shifting from using a permanent water source in the dry season (Lake Victoria and the Rubana River, respectively) to utilizing seasonal ponds and swamps or nearer streams/seasonal rivers in the wet season. Therefore, in the dry season in both regions, both the distance and direction of grazing movements is dictated in large part by the necessity of travelling to the sole dry season water source (Coppolillo 2000). In addition, Coppolillo (2000) found that herders in his study region showed a preference for high density settled areas in both seasons: in dry, this was due to grazing activities centered on the household's harvested fields, and in wet, to the maintenance of short grazing lawns in settled areas. This too is similar to seasonal grazing habits in this study's focal villages; however, the use of harvested fields was not always limited to the household's own fields. Yet while permission to graze in a neighbor's harvested field seemed to be universal in Mwamalole sub-village, it was variable among respondents in Nyamisisi, with just under 65% of respondents citing access. Nyamisisi residents claimed that farmers could choose to prohibit livestock access and that permission to graze depended upon your relationship to a particular farmer. They further explained that sometimes cows may eat a farmer's crops (in the wet season) and this can lead to conflicts between farmers and pastoralists, often leading to reduced access to harvested fields (Chapter 3). This issue is a particularly large problem for those livestock owners practicing solely pastoralism with no farm fields of their own. Further, while permission to settle and farm within a village must be granted from the village officers, there is, as yet, no real system of land ownership, with settlers instead able to 'claim' whatever land they have developed either by building a house or sowing a field.

Fernandez-Gimenez (2000) similarly found that political and socioeconomic factors often prevent Mongolian pastoralists from being able to use their ecological knowledge in making grazing management decisions and that this often results in poor or disadvantaged herders violating traditionally held pasture norms, such as grazing in winter reserves during summer, etc. (Fernandez-Gimenez 2000). Baker & Hoffman's (2006) study of herders in South Africa also found land tenure and individual income to be among the significant factors influencing herding strategy and movement decisions. Collectively, these studies reveal that the practicality and efficiency of a particular herding strategy should be assessed in the context of the herder's livestock production goals and that it depends heavily on the individual herder's personal constraints posed by economic and other personal factors in conjunction with those posed by variable climatic and environmental factors (Baker & Hoffman 2006).

Based on the above findings, particularly from Chapter 2 and the related literature, it appears that preserving the resilience of a system being managed for livestock grazing may be best achieved by adopting a system of rotational grazing that more closely mimics the short, intense bouts of grazing followed by periods of rest typified by wildlife-grazed systems (such as that typified by traditional transhumant societies (Niamir-Fuller & Turner 1999; Turner & Niamir-Fuller 1999; Turner *et al.* 2014)), rather than by merely lowering livestock numbers or overall grazing intensity (Chapter 2). However, in systems where livestock are managed by independently-motivated individuals, rather than as a collective group, this ideal may prove difficult to attain (Chapter 3). In these systems, such as the Kijereshi and Nata/Isenye regions of the GSE (Chapters 2 & 3), grazing management could be aided by a communal 'grazing committee' charged with the task of managing the cohesive movement of communal herds across the landscape. In a study of the 'sustainability of pastoralism' in the western Himalayas, Casimir and Rao (1998) found that only those pastures with no recognized legitimate ownership (albeit private, communal, government, or even spiritual) faced livestock numbers with requirements beyond what was available in the pasture. In this sense, they argue that privately or communally owned pastures can indeed be "sustainable" whereas those left as "no-man's land" are more likely to be overstocked and undergo degradation (Casimir & Rao 1998). This model of communal grazing management has already been successfully put into practice in other regions, including across the community conservancies of northern Kenya (Northern Rangelands Trust 2013). Furthermore, many studies have shown that pastoralists have a vast ecological knowledge regarding specific plant species and their characteristics (Fernandez-Gimenez 2000) and that they use key plant species indicators (those that are important as fodder for different livestock species) as well as various livestock productivity indicators such as body condition and reproductive performance to monitor grazing effects on rangelands (Roba & Oba 2009). They have also been found to differentiate between seasonal effects and those representing persistent degradation and to use this ecological information in making herding decisions at various spatial and temporal scales (Fernandez-Gimenez 2000).

However, while communal grazing plans may help to preserve ecosystem resilience by redistributing the intensity of grazing impacts over a larger spatial and smaller temporal scale, collective management also presents additional challenges such as enforcement of grazing policies (Nilsson 2001), particularly in communities that lack cultural norms of sharing land or where such systems have begun to degrade due to increased overlap of grazing areas with other ethnic groups and/or a shift from traditional values within the community. Fernandez-Gimenez (2000) proposes institutions that regulate mobility (regulating how the resource is used [*i.e.* regulating when, where, and for how long grazing may occur] rather than allocating it to specific users) over a formal property rights system.

She argues that by fostering mutual expectations regarding herder behavior, these institutions can regulate resource use as well as formal tenure systems while also allowing for the necessary spatial and social mobility and flexibility. With a lack of or weakening in such institutions, Fernandez-Gimenez found that Mongolian herders will tend to violate pasture use norms in order to protect individual access to key resources (*i.e.* winter or spring grazing reserves, summer camps, etc.). She further found that flexible access to forage reserve outside one's customary area was more important to herders than exclusive, formal rights to pasture, which they saw as threatening or restricting this flexibility of access (Fernandez-Gimenez 2000).

Fernandez-Gimenez's findings and recommendations from Mongolia resonate with the broader framework for managing the sustainability of common property resources within social-ecological systems proposed by the late Nobel- prize winning economist, Elinor Ostrom (Ostrom *et al.* 1999; Dietz *et al.* 2003; Ostrom 2007). Ostrom and colleagues have found, through case studies across a wide range of environments, that self-governing institutions are most successful at managing common property resources when a series of conditions are met (Dietz *et al.* 2003; Ostrom 2007). First, the resources and its use should be able to be easily monitored; for grazing resources, this can be achieved through repeated scientific measurements of grass quantity and quality including indices of composition, diversity and richness, as well as for water resources through measurements on flow rates or aspects of water quality. Second, rates of change in resources, users and other social and economic conditions should be moderate(Dietz *et al.* 2003); in communities experiencing a rapid influx of immigrants (additional resource users), successful management becomes more difficult. A third requirement for successful common property resource management is that resource users engage in frequent social interaction that builds trust and raises the likelihood of compliance with agreed-upon restrictions(Dietz *et al.* 2003). Tightly-knit pastoral communities will likely find this easier to achieve than communities made up of a more diverse mix of people with various, and sometimes competing, livelihood goals. The fourth condition is probably the most difficult for communities like those in the Kijereshi and Nata/Isenye regions of the GES to meet and that is the ability to exclude outsiders from using the resource. Dietz and colleagues note that new entrants to the resource-user population 'add to the harvesting pressure and typically lack understanding of the rules' (Dietz *et al.* 2003) and according to survey respondents from Mwamalole and Nyamisisi sub-villages (Chapter 3), this has certainly been the case in these regions (Nata/Isenye especially) where continually increasing numbers of new settlers from other regions (often with large numbers of livestock) build mounting pressure on grazing resources and pose as a large threat to a successful system of communal management. Finally, individual users should take action to support monitoring and enforcement (Dietz *et al.* 2003); in grazing lands, this could mean herders simultaneously acting as security patrol while out with livestock and reporting those they observe to be breaking the rules.

An additional challenge in incorporating communal grazing management plans lies with those communities that lack a large enough total area within which to sustain their animals using rotational grazing activities and still allow for adequate rest periods. Thus, while communities may be successful in pooling their herds together and executing intense grazing rotations, their total collective land area may be insufficient to sustain the herds throughout the year without needing to return to 'overgraze' some areas meant to be in recovery. In Laikipia, Kenya, this is often buffered by land-sharing agreements with neighboring private ranches (pers. obs.). In other areas, arrangements could possibly be made for dry-season grazing access in neighboring game reserves, though this would need to be adequately enforced.

Allowing livestock owners temporary, seasonal access to private ranches or game reserves is a controversial issue and one that would need to be considered carefully on a case-by-case basis. However, the outcome of maintaining healthier, more resilient grasslands outside protected areas are many: livestock owners benefit through greater access to grazing resources that allows them to continue their pastoralist or agropastoralist livelihood, which in turn limits the spread of agriculture onto grazing lands shared by livestock and wildlife both. Preservation of pastoralist livelihoods could serve to stem the 'pre-emptive farming' often practiced by landowners living adjacent to protected areas, who "farm as much as possible" out of fear of losing land to conservation in order to ensure they receive just compensation in the case of eviction (Goldman 2009) and instead protect grazing land from conversion. Particularly for those who have already faced an eviction, such as those respondents in Isenye region who formerly lived in what is now Grumeti Game Reserve (Chapter 3), this is a valid fear that seasonal access to grazing resources within the protected area could help assuage. Establishing joint wildlife-livestock grazing areas and stemming the spread of farming onto existing grazing areas would provide benefits to wildlife conservation as well as it would help to ensure the "permeability of the intervening matrix" between two (or more) protected conservation areas (Goldman 2009). In the area surrounding Tarangire National Park in northern Tanzania, joint wildlife-livestock grazing areas are proving to be the most ecologically appropriate and politically acceptable option for preserving or restoring the connectivity between protected areas that wildlife often require (Goldman 2009).

As the Greater Serengeti ecosystem's tropical climate and C_4 grasslands are likely best managed at high levels of grazing (Chapter 4), increasing grazing intensity in areas currently being underutilized (as is potentially the case in some game reserves) could not only help to resolve pastoralist issues of limitations on space and movement options, but also potentially increase SOC levels and possibly generate additional revenue to support pastoralist livelihoods. This outcome would represent a multiple 'win' situation, as it would help to preserve traditional livelihoods that are compatible with wildlife conservation, maintain ecosystem resiliency and function for both domestic and native herbivores, and potentially help to mitigate the effects of global climate change.

In conclusion, while this manuscript has covered a seemingly broad array of topics, hopefully it has also emphasized a significant connection between the "anthropogenic processes driving resource use and the resultant landscape-level changes" (Coppolillo 2001) and the consequent usefulness of expanding our research toolbox in order to link ecological studies to those that explore the many sociological, economic, cultural and historical influences on the human actors within the system. With so few "untouched" ecosystems left on earth, it is imperative that any study of ecology or the environment recognize and take into account the far-reaching influence of humans and in the combined human-natural systems surrounding national parks like Serengeti and other wildlife-rich regions of Africa, this is becoming impossible not to do. Based on what I've learned from these studies and from the literature, it seems the most important attribute for preserving ecosystem resiliency is flexibility in land use practices. When land users are able to choose from a variety of options, they are better able to sustainably manage their lands and preserve the compatibility of pastoralism and wildlife conservation. Thus, while many of the results from these studies are particular to this system, a number of these conclusions-including the importance of recognizing both the broad environmental and the specific management context of a system and incorporating flexibility into management practices-can be applied in other, related systems and it is the hope that this thesis has added to the body of work on grazer impacts in a positive and informative way.

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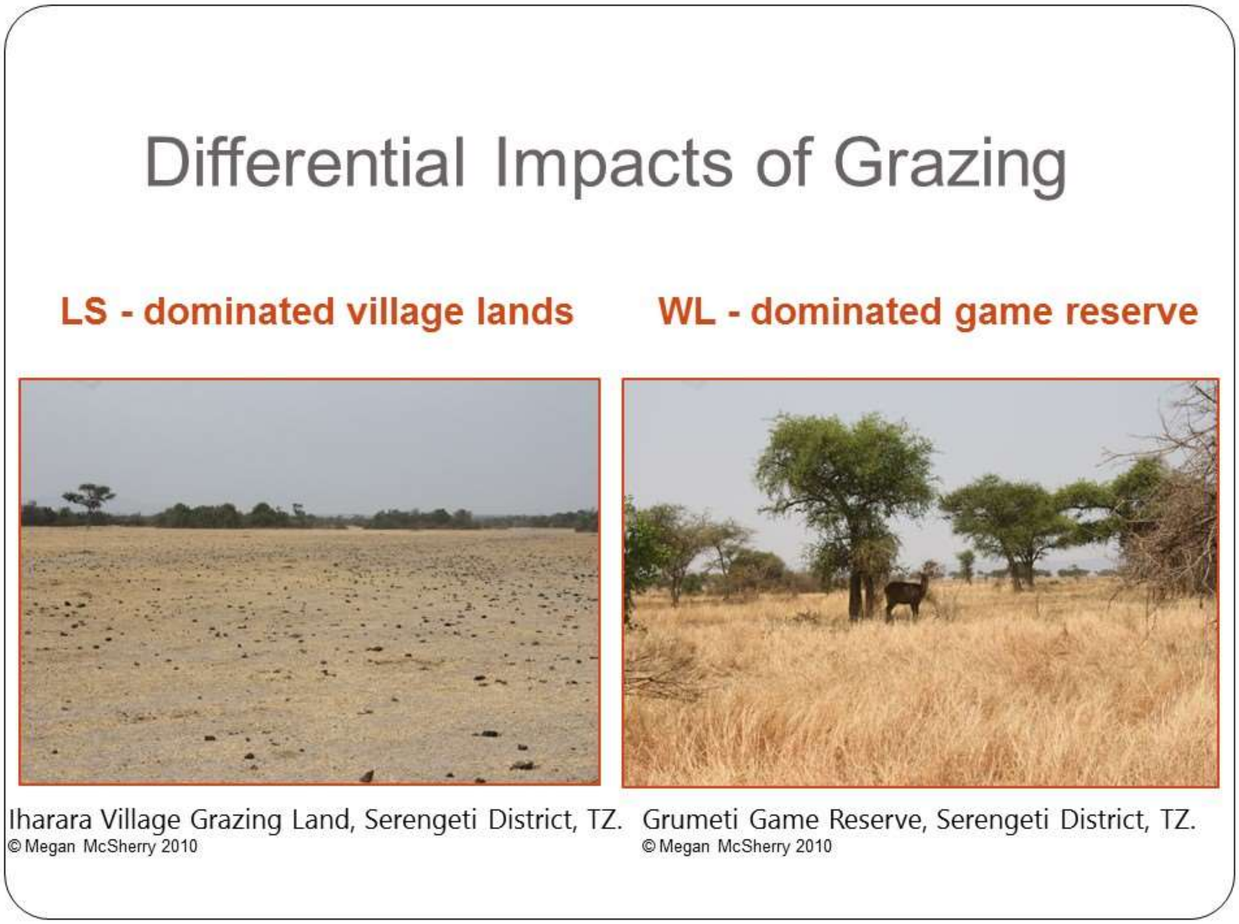
FIGURE CAPTIONS

Figure 1. Images showing the visual differences in vegetation on lands grazed by livestock and those grazed by wildlife within the Greater Serengeti Ecosystem. These images were taken two days apart in the same year (2010) and were located less than 800 meters from one another, on either side of the Rubana River border that separates Grumeti Game Reserve from Iharara village grazing land within the Isenye study region of Chapters 2 & 3.

Figure 1.



Differential Impacts of Grazing

LS - dominated village lands

WL - dominated game reserve

Iharara Village Grazing Land, Serengeti District, TZ.
© Megan McSherry 2010

Grumeti Game Reserve, Serengeti District, TZ.
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SUPPLEMENTAL INFORMATION

S1. Core species (by region) identified at the end of wet season 2 (April 2012) by determining the percentage of a species' presence in livestock-grazed and wildlife-grazed plots. A species was included in the regional set if it was present in >20% of all plots or >25% of all plots within one management type (Chapter 2).

S2. Individual herder questionnaire on livestock movement and management (Chapter 3).

S3. Oral consent form introducing the researchers, explaining the study, and outlining the low-risk and voluntary nature of participation in the herder questionnaire (Chapter 3).

S4. Translation of oral consent form into Kiswahili, the *lingua franca* spoken among study participants in both regions (Chapter 3).

S5. Model descriptions and model selection results of full set of 18 models in the meta-analysis, based on Akaike Information Criterion with small-sample bias adjustment ($\mathrm{AIC_C}$) and AIC weights (w_i) (Chapter 4).

S6. Detailed explanation of the use of AIC weights (w_i) in model selection (Chapter 4).

S1.

Table S1.1. Set of core species found in the Kijereshi region in April 2012.

Species	Functional Group
Sporobolus ioclados	Grass
Chrysochloa orientalis	Grass
Microchloa kunithii	Grass
Sporobolus nervosa	Grass
Themeda triandra	Grass
Panicum coloratum	Grass
Sporobolus pyramidalis	Grass
Brachiaria semiundulata	Grass
Commelina species	Forb
Portulaca species	Forb
Indigofera hochstetteri	Forb
Justicia matamensis	Forb
Sedge species	Sedge

Table S1.2. Set of core species found in the Nata/Isenye region in April 2012.

Species	Functional Group
Themeda triandra	Grass
Panicum coloratum	Grass
Chrysochloa orientalis	Grass
Sporobolus pyramidalis	Grass
Sporobolus pellucidus	Grass
Sporobolus festivus	Grass
Sporobolus ioclados	Grass
Bothrichloa insculpta	Grass
Digitaria macroblephara	Grass
Brachiaria semiundulata	Grass
Indigofera volkensii	Forb
Indigofera hochstetteri	Forb
Ipomea mombassana	Forb
Commelina species	Forb
Crotalaria spinosa	Forb
Sedge species	Sedge

S2.

Livestock Movement: Factors Influencing Herder Decision-Making[1]

Interviewers: ______________________________

Survey #: ____

Time: ________

Date: ________

Location: ______________________________

Place Name: ______________________________

General Category (circle one)

1) agricultural area

2) pastoral/grazing area

3) trading center/town

4) other ______________________________

GENERAL INFORMATION of person being interviewed (Questions 1-7a)

Sex

1) female 2) male

Age:

---

[1] **This survey instrument is intended for use with individual subjects but may also be used in a group interview setting. In both cases, no names or other identifiable information will be collected.**

What is your age?

1) 0-19 2) 20-29 3) 30-39 4) 40-49 5) >49

Tribe/Ethnicity

1) Sukuma 2) Nata 3) Ikoma 4) Other_________________________________

*Marital Status

1) single 2) married 3) widowed 4) other ______________ # spouses__________

*What is your highest level of education reached? If completed, check here _____

1) none 2) primary 3) secondary 4) university 5) post-university

What is your primary economic livelihood?

1) agriculture 2) pastoralism 3) agro-pastoralism

4) other – specify (teacher, storeowner, guard, etc...) __________________________

Do you (or does the head of your family) own livestock? 1) yes 2) no

(If no, end of survey. If yes, continue to next question.)

How many people are supported by this herd (*i.e.* number of people in household dependent on livestock owner)? ______________

POPULATION DYNAMICS (Questions 8-14a)

How long have you lived in this area? (please write specific number as well) __________

1) 0-6 months

2) 6 months to a year

3) 1-5 years

4) 6-10

5) 11-20

6) 21+

7) life

How much longer do you plan on living in this area? (please write specific number as well)

1) 0-6 months

2) 6 months to a year

3) 1-5 years

4) 6-10

5) 11-20

6) 21+

7) life

If did not answer “life”, please ask why plan to leave this area.

Write answer: ____

Do you think there are more or less people here than in the past?

1) more   2) less   3) no change   4) don’t know

Why do you think this is happening?

How would you classify the density of people in this area?

1) low 2) moderate 3) high

Do you think there are more or less livestock here than in the past?

1) more 2) less 3) no change 4) don't know

Why do you think this is happening?

How would you classify the density of livestock in this area?

1) low 2) moderate 3) high

Do you think livestock-keeping will be successful in this area in the future (10-20 years)?

1) yes 2) no

Why or why not? ____

GENERAL LIVESTOCK INFO (Questions 15-25)

For what purpose do you keep livestock?

1) subsistence 2) commercial 3) both 4) other: ______________________________

How many do you own of each… Cattle? _______ Sheep? ________ Goats? ________

Donkeys? ________ Other? ____

How did you acquire your cattle? (select as many as apply)

1) Bought 2) Traded 3) Inherited 4) Dowry 5) Was given as a gift 6) Other

If other, explain: ____

Who is responsible for herding livestock (list all if more than one person)?
____

What is their age? _______ Relation to head of household? ________________________

How many people total contribute to the herding or other management of your herd? #_____

Are your livestock herded together with another livestock owner?

1) Yes 2) No

If yes, how many families (heads of household) herd their livestock together? ___________

Are cattle and shoats herded separately or together? ______________________________

Are herds split in any other ways (circle all that apply)?

1) Calves herded separately 2) Calves herded with small stock

3) Lactating females herded separately 4) Other _________________________________

What is the total number of livestock that are herded together?

1) 0-20 2) 21-50 3) 51-100 4) 101-200 5) 201-500 6) 500+

Write number here: _________

Are herds ever moved outside the village area?

1) yes 2) no

What is the main factor influencing a decision to move?

1) Season 2) Lack of sufficient water 3) Lack of sufficient pasture 4) Other

If other, write here: ____

HERD MOVEMENT (Questions 26-42)

Who is the primary decision-maker regarding herd movement? ____________________

If person answers him/herself:

How do you decide when and where to move livestock around for grazing? ___________
____

____

Who decides where to take herd each day? _____________________

Are herds taken to and from one site or moved from place to place over the course of a day?
____

Do herds travel along fixed routes dictated by primary decision-maker or are movement decisions made by herder as he/she goes? ________________________________

____

What is the farthest distance from home herds will travel in a day? _______________

What is the average total distance herds will travel in a day? (write specific number as well)

1) 0-5 km 2) 6-10 km 3) 11-15 km 4) 16-20 km 5) 21-25 km 6) > 25 km

How is grazing distributed around the homestead? ___________________________

____

What factors influence where to take herds? List and rank importance, 1 being highest:

_______________________________ _____

_______________________________ _____

_______________________________ _____

_______________________________ _____

_______________________________ _____

_______________________________ _____

How important are the following in deciding where to move herds?

1) Vegetation color very important somewhat important not important
2) Vegetation height very important somewhat important not important
3) Vegetation type very important somewhat important not important
4) Vegetation density very important somewhat important not important

How is vegetation quality assessed? ____

Describe any differences associated with herding practices/grazing patterns between seasons. ____

____
____

Where are herds taken to water in dry season?

1) Well 2) River 3) Pond/Lake/Swamp 4)Pipeline/Borehole 5) Other_________

Where are herds taken to water in wet season?

1) Well 2) River 3) Pond/Lake/Swamp 4) Pipeline/Borehole 5) Other_________

How often are herds taken to water? Dry: Cattle_______________ Shoats_______________
Wet: Cattle_______________ Shoats_______________

What other factors contribute to whether a grazing area is considered 'good' or 'bad'?
____

What factors (ecological, economic, political, personal, or other) restrict movement (either day-to-day or over longer time scales)? ____

____

____

How does decision-maker acquire information regarding suitability of distant grazing sites?

____

PERCEPTIONS (Questions 43-53)

How soon will you come back to an area after the grass has been depleted?

Dry:_________________________________Wet:_______________________________

How would you classify water availability in the area? ____________________________

How big of a risk do you feel is associated with diseases from wildlife?

1) no risk 2) small risk 3) moderate risk 4) big risk 5) extremely big risk

What actions do you take to prevent disease from wildlife?

1) vaccination 2) dipping 3) stay far from wildlife 4) other ____________________

When wild herbivores are present, what is the minimum distance you keep between them and your herd?

1) 0-10 m 2) 11-25 m 3) 31-50 m 4) 50-100 m 5) 100-200 m 6) > 200 m

How likely are you to bring your livestock into a protected area to graze?

1) Very likely 2) Somewhat likely 3) Not at all likely 4) Only likely during severe drought 5) Other Explain: ____

How important is the following in deciding whether or not to bring livestock to graze in a protected area?

Higher-quality vegetation in P.A.	very important	somewhat important	not important
Higher-quantity vegetation in P.A.	very important	somewhat important	not important
Distance from home	very important	somewhat important	not important
Proximity to (or distance from):			
Ranger post	very important	somewhat important	not important
Gate	very important	somewhat important	not important
Tourist camp/lodge/hotel	very important	somewhat important	not important
Water source	very important	somewhat important	not important

What do you feel is the risk associated with grazing in a protected area?

1) no risk 2) small risk 3) moderate risk 4) big risk

What are some of the risks associated with grazing in a protected area?
____

How often do the following types of conflicts occur in the area where you graze your stock?

Competition over grass	not at all	rarely	often
Competition over water	not at all	rarely	often
Predation of livestock	not at all	rarely	often
Destruction of crops	not at all	rarely	often

Are there other conflicts that deter herders from grazing herds in certain areas (i.e. conflicts with farmers, other herders, park management, etc.)?

1) Yes 2) No Explain: ____

ADDITIONAL COMMENTS:

S3.

Livestock Movement: Factors Influencing Herder Decision-Making

Hello, my name is Megan McSherry and I am a researcher from Syracuse University in the United States. I am conducting research here today with permission from TAWIRI (Tanzania Wildlife Research Institute) and the Tanzanian Commission of Science and Technology (COSTECH). This research aims to understand how livestock owners make decisions about how to herd their livestock and what types of things affect these decisions. We would like to understand the types of things that influence where and when livestock are moved across the land in order to get a better idea of how the pattern of livestock grazing affects the plants and soil. This knowledge will help us understand changes in plant communities and soil nutrients and possibly expose an opportunity for additional revenue to be brought to communities through soil carbon storage projects (storing air in the soil). We are interviewing people over the age of 18 years old in your village and in neighboring villages whose families keep livestock. I am inviting you to participate in this study. If you choose to participate, you will be asked about the composition and size of your family's livestock herd, who is responsible for moving the herd around, and how that person decides where to take livestock each day. You are free to refuse to participate, to not respond to any questions you do not wish to answer, and to stop answering questions at any time you wish. The survey should take approximately 1 hour of your time. I will not ask for your name and all of your information will be kept confidential. We do not foresee any risk to you in answering these questions but if you feel uncomfortable in answering any question, you may choose not to respond. What I have just said is available on paper if you would like a copy and if at any point during the survey or after you would like further information, feel free to ask me or any other member of the research team. Do you agree to participate in this study? Do you have any questions before I begin?

For further information, please contact:

Megan McSherry	0685464711	megan.mcsherry@gmail.com
Emilian Mayemba	0784653515	mayembaemilian@yahoo.co.uk

S4.

Habari, mimi ni Megan McSherry na mimi ni mtafiti kutoka Chuo Kikuu cha Syracuse cha nchini Marekani. Ninafanya utafiti hapa leo kwa rushusa kutoka TAWIRI (Tanzania Wildlife Research Institute) na Tume ya Sayansi na Teknolojia ya Tanzania. Utafiti huu unakusudia kuelewa namna ambavyo wafugaji wanafanya maamuzi jinsi ya kuchunga mifugo na vitu ambavyo vinaathiri maamuzi haya. Tungependa kuelewa vitu ambavyo vinaathiri wapi na lini mifugo inahamishwa ili kupata njia bora ya jinsi ufugaji unvyoathiri ardhi na mimea. Maarifa haya yatatusaidia kuelewa mabadiliko katika jamii za mimea na virutubisho vya udongo na labda kutafuta fursa za kipato cha ziada kupitia uhifadhi wa hewa kwenye udongo. Tunahoji watu wenye miaka kumi na nane au zaidi katika kijiji chako na vijiji vya jirani ambavyo familia zao zinachunga mifugo. Ninakuomba kushiriki katika utafiti huu. Kama utachagua kushiriki, utaulizwa kuhusu mifugo ya familia yako, nani anahusika kuchunga mifugo, na jinsi ambavyo mtu huyo huamua wapi apeleke mifugo kila siku. Upo huru kukataa kushiriki, au kutojibu swali lolote ambalo hutaki kujibu, au kuacha kujibu maswali wakati wowote utakapojisikia. Utafiti utachukua walau saa moja. Sitauliza jina lako na taarifa zako zote zitakuwa ni siri. Hatuoni tatizo lolote kwa wewe kujibu maswali haya lakini kama unasikia wasiwasi katika kujibu maswali haya, unaweza kuamua kutojibu. Maelezo haya yapo kwenye karatasi kama ukitaka nakala na kama katika hatua yoyote wakati wa maswali au baada ya maswali ungependa taarifa zaidi, upo huru kuniuliza mimi au mtafiti yeyote. Ungependa kushiriki katika utafiti huu? Una maswali yoyote kabla ya kuanza?

Kwa taarifa zaidi:

Megan McSherry	0685464711	megan.mcsherry@gmail.com
Emilian Mayemba	0784653515	mayembaemilian@yahoo.co.uk

S5.

Model Descriptions:

1) Full model including all six variables (mean annual precipitation, soil type, dominant grass type, grazing intensity, sampled soil depth and study duration) and the three interaction terms (precipitation x soil type, grass type x grazing intensity, depth x duration)

2) Just main effects

3) Just interactions

4) Environmental variables alone

5) Biotic variables alone

6) Design variables alone

7) Environmental and design variables

8) Biotic and environmental variables

9) Biotic and design variables

10) Biotic and design variables plus mean annual precipitation

11) Biotic and design variables plus soil type

12) Environmental and design variables plus grass type

13) Environmental and design variables plus grazing intensity

14) Environmental and biotic variables plus sampled soil depth

15) Environmental and biotic variables plus study duration

16) Our hypothesized best model- similar to full model but excluding grazing intensity and study duration main effects

17) Environmental variables plus grass type and sampled soil depth main effects

18) Environmental variables plus biotic and design interactions

Table S5.1. Model selection results from set of 18 candidate models in the meta-analysis, based on Akaike's Information Criterion with small-sample bias adjustment (AIC$_C$) and AIC weights (w_i).

	Model	K[a]	SSE[b]	AIC$_C$[c]	Δ_i[d]	w_i[e]
16	P[f], S[g], PxS[h], G[i], GxGI[j], D[k], DxDu[l]	8	0.164	-246.14	0.00	0.897
3	PxS, GxGI, DxDu	4	0.235	-240.07	6.07	0.043
1	P, S, PxS, G, GI[m], GxGI, D, Du[n], DxDu	10	0.164	-239.82	6.32	0.038
18	P, S, PxS, GxGI, DxDu	6	0.217	-238.67	7.47	0.021
15	P, S, PxS, G, GI, GxGI, Du	8	0.236	-229.03	17.11	1.73x10^{-4}
8	P, S, PxS, G, GI, GxGI	7	0.252	-228.87	17.27	1.59x10^{-4}
14	P, S, PxS, G, GI, GxGI, D	8	0.249	-226.51	19.63	4.91x10^{-5}
12	P, S, PxS, D, Du, DxDu, G	8	0.316	-215.31	30.83	1.82x10^{-7}
17	P, S, PxS, D, G	6	0.385	-211.72	34.42	3.01x10^{-8}
7	P, S, PxS, D, Du, DxDu	7	0.401	-207.03	39.10	2.89x10^{-9}
4	P, S, PxS	4	0.480	-206.50	39.64	2.22x10^{-9}
13	P, S, PxS, D, Du, DxDu, GI	8	0.399	-204.35	41.79	7.57x10^{-10}
11	G, GI, GxGI, D, Du, DxDu, S	8	0.423	-201.61	44.53	1.92x10^{-10}
2	P, S, G, GI, D, Du	7	0.522	-194.64	51.50	5.89x10^{-12}
5	G, GI, GxGI	4	0.861	-179.04	67.10	2.41x10^{-15}
9	G, GI, GxGI, D, Du, DxDu	7	0.744	-177.98	68.15	1.42x10^{-15}

10	G, GI, GxGI, D, Du, DxDu, R	8	0.723	-176.41	69.73	6.49×10^{-16}
6	D, Du, DxDu	4	0.956	-174.12	72.02	2.06×10^{-16}

In table, a= number of parameters in the model, including intercept; b= sum of squares error in the model; c= Akaike's Information Criterion (AIC) (Akaike 1985, Burnham & Anderson 1992) with the small-sample bias adjustment ($AIC_C = n*[\ln(SSE/n)]+2K + [(2K(K+1)) / (n - K - 1)]$) (Hurvich & Tsai 1995, Burnham and Anderson 2002); d= difference in AIC value between each model in the set (model *i*) and the best model : $AIC_i - AIC_{min}$; e= AIC weight, $w_i = \exp(-0.5 * \Delta_i) / \sum_{r=1}^{R} \exp(-0.5 * \Delta_i)$ (Burnham & Anderson 2002); f= Mean annual precipitation (mm); g= Soil texture type (see Methods for category descriptions); h= an interaction term for precipitation and soil type; i= Dominant grass species type (C_3, C_4, or mixed); j= an interaction term for grass type and grazing intensity (light, moderate, or heavy); k= Sampled soil depth (cm), l= an interaction term for soil depth and study duration (years); m= Grazing intensity; and n= Study duration.

S6.

Akaike's Information Criterion (AIC) is a measure of the relative goodness of fit of a model (Akaike 1974, 1985). It offers a relative measure of the amount of information lost when a particular model is used to explain reality, illustrating the tradeoff between bias and variance in the construction of a model. More generally, it captures the tradeoff between the model's accuracy and its complexity (Burnham & Anderson 1992). AIC values offer a means for model selection by allowing one to examine each candidate model's relative distance to the "truth," or what is actually happening in reality. AIC scores are derived from the maximum value of the likelihood function of the model (with the equation $AIC = 2K - 2 * \ln(L)$) but can also be derived using sum of squares error (SSE) with the formula $AIC = n * [\ln(SSE / n)] + 2K$ (Burnham & Anderson 2002), where n is the sample size and K is the number of model parameters, including the intercept. AIC values that may be biased by either a small sample or a high number of parameters with respect to sample size should typically then be adjusted by the small-sample bias adjustment ($AIC_C = AIC + 2K * (K + 1) / (n - K - 1)$) (Hurvich & Tsai 1995). This adjustment corrects for the lack of balance between number of parameters and sample size which could otherwise increase the probability of selecting a model with too many parameters. The model with the lowest AIC_C value is chosen as the best model. However, AIC and AIC_C can only be used in comparing one model to the next; these values give no indication of the absolute fit of the model to the data (Burnham & Anderson 2002). They merely illustrate differences in goodness of fit between competing models.

To further aid in selection of a best model from a set of candidate models, Akaike information criterion *weights* can be used. AIC weights (w_i) represent the "weight of evidence" in favor of model *i* being the best approximating model in the set (Burnham & Anderson 2002). AIC weights serve to normalize the relative likelihood values of a set of models and are calculated using the formula $w_i = \exp(-0.5 * \Delta_i) / \sum_{r=1}^{R} \exp(-0.5 * \Delta_i)$, where w_i is the weight for model *i*, Δ_i is the difference in AIC value between model *i* and the best model (*i.e.* the model with the lowest AIC), and the denominator is the sum of the relative likelihoods for all candidate models (Burnham & Anderson 2002). The model with the highest AIC weight represents the best model in the set.

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VITA

Megan E. McSherry was born and raised in Syracuse, New York. After completing her secondary education at Thomas J. Corcoran High School in 2002, she attended Cornell University's College of Agriculture & Life Sciences where she majored in Natural Resources and minored in Development Sociology and International Development. In her junior year, she studied abroad at the School for Field Studies' Center for Wildlife Management Studies in Kenya. She graduated from Cornell in 2006 with a Bachelor of Science. During the following two years, she worked as an environmental educator at centers in Fairhope, Alabama, New Canaan, Connecticut, and Fort Bragg, California. She also spent several months abroad volunteering on wildlife research projects, first with The Peregrine Fund in Soberañia National Park, Panama and then with the Hlami Association for Turtle Conservation and Hope (HATCH) in Ada Foah, Ghana. In August 2008, Megan entered the Graduate School of Syracuse University where she enrolled in the Biology Department's PhD program and began her studies that culminated in this work.