

To the University of Wyoming:

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The hirola (*Beatragus hunteri*) is one of the rarest antelopes on Earth, with a global population size of ca. 500 individuals restricted to 1500 km<sup>2</sup> on the Kenya-Somalia border. Hirola has exhibited ongoing declines since the 1970s while the remaining populations occur almost solely on pastoral lands with no formal protection. Because of historical and political instability in the hirola's native range, it has been difficult to clearly identify the reasons underlying hirola declines. Like many other globally endangered species, it is likely that more than one factor underlies the hirola problem. Therefore, I investigated, 1) the role of predation and range degradation in driving hirola declines, 2) mechanisms responsible for hirola range collapse and landscape change within hirola historical range, and 3) identified socially-acceptable strategies for habitat restoration and hirola recovery. I have used a combination of GPS telemetry, analysis of long-term satellite imagery, a large-scale predator exclusion zone, and structured questionnaires to address my objectives. Understanding the impacts of these factors can help determine the next steps necessary to maximize the chances of hirola persistence in the future. My findings suggest that, a combination of top-down (predation) and bottom-up (rangeland quality) forces drive hirola declines, with populations in the historical range being impacted more by poor rangeland quality. Additionally, resource selection analysis revealed that contemporary low numbers of hirola are due to loss of forage via tree encroachment. Some factors—including mega-herbivore extirpations, fire suppression, and overgrazing—were likely to have triggered tree encroachment which may be slowing contemporary recovery efforts. Local communities supported efforts to conserve elephants,

seed and fertilization of grass, and removal of trees as means to restore hirola historical range. However, the locals were opposed to voluntary reduction of livestock and were ambivalent towards soil ripping and control burns. Livestock wealth (ownership) and years of residency were important predictors of locals' perceptions toward rangeland-restoration practices. I recommend a combination of rangelands restoration efforts that have local support coupled with reintroductions to enhance the chances of recovery for this globally endangered species.

**RANGE COLLAPSE, DEMOGRAPHY AND CONSERVATION OF THE  
CRITICALLY ENDANGERED HIROLA ANTELOPE IN KENYA**

By

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in

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by

Abdullahi H. Ali

This dissertation is solely dedicated to my late brother Muhumed H. Ali who lost his life in a surgical theatre room at the Garissa General hospital (Kenya) in October 2004. May God rest his soul in eternal peace. Amen.

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## Chapter 1

### Demographic drivers of the worlds' most endangered antelope: matrix models guide strategies for reintroductions

#### 1.1 Introduction

Global extinction of species has been rising over the last century, reflecting the lasting imprint of human activities (Grehan 1993; Hoekstra *et al.* 2005; Laurance 2007; Clausnitzer *et al.* 2009; Şekercioğlu *et al.* 2011; Barnosky *et al.* 2012; Dirzo *et al.* 2014). As a consequence of habitat loss, over-exploitation, and climate change, many species are increasingly vulnerable to extirpation or wholesale extinction as small populations succumb to demographic stochasticity. There is evidence suggesting that contemporary rates of species loss are higher than in prehistoric times (Beever *et al.* 2011; Ceballos *et al.* 2015), and that higher-order taxa are being lost at unprecedented rates (McCallum 2015). For example, and over the past century, the Earth has borne witness to the loss of several mammalian genera, including a genus of marine herbivore (*Hydrodamalis*; Turvey and Risley 2006), a genus of a desert rat kangaroo (*Caloprymnus*; Fisher 2011) and a genus of marsupial carnivore (*Thylacinus*; Prowse *et al.* 2013).

The forces that affect wildlife populations—and thus extirpation and eventual extinction—combine bottom-up and top-down processes that are dynamic in space and through time. Understanding of these processes can be used to steer conservation efforts (Sinclair & Krebs 2002; Wallach, Ripple & Carroll 2015). While understanding top-down and bottom-up control is critical for reintroductions, recovery efforts often are conducted without an *a priori* understanding of the relative roles of these processes, leading to reintroductions that are



inadequate or ineffective (Balmford & Cowling 2006; Meijaard & Sheil 2007; Tanentzap, Kirby & Goldberg 2012; Morrison 2013). In light of the widening gap between conservation efforts and continued declines in populations, the conservation community has started to evaluate the effectiveness of management interventions by explicitly quantifying their impact on population growth of species of conservation concern (e.g., Beale *et al.* 2013; Tulloch *et al.* 2015). While the escalation of extinction risk has led to heightened urgency to identify effective conservation efforts, many efforts still fail to incorporate evidence-based practices that could increase their effectiveness (Sutherland *et al.* 2004).

The hirola antelope (*Beatragus hunteri*) is a critically endangered species from a once-widespread lineage, having declined from over 15,000 individuals to <500 individuals today (IUCN 2008). While there is uncertainty as to why hirola populations have declined since the 1970s, some have speculated that a combination of heightened predation and reduced rangeland quality is responsible for its distinction as the world's most endangered antelope (Probert *et al.* 2015). Such uncertainty characterizes the plight of many species of conservation concern, and can translate to variable outcomes in reintroduction efforts (Sarrazin & Barbault 1996; Milner-Gulland *et al.* 2003; Sutherland *et al.* 2004; Armstrong & Seddon 2008). To date, recovery efforts for hirola have occurred mostly through community-based conservancies and sanctuaries (e.g., the Ishaqbini Community Conservancy in eastern Kenya; Measham & Lumbasi 2013). While these recovery efforts have had some success, the vast majority (>90%) of hirola occur outside conservancies or formally protected areas, where they co-exist with pastoralists, livestock, and a suite of large carnivores.

Vital rates encompass the survival, growth, and reproduction of individuals through their lifetimes, and the response of these vital rates to environmental variation determines

population dynamics. Therefore, I sought to quantify the relative importance of vital rates (agespecific survival and fecundity) to population growth of hirola, with the intent of centering recovery plans on the processes most likely to reverse population decline (Johnson *et al.* 2010). Between 2012 and 2015, I quantified vital rates within (1) a predator-proof sanctuary with relatively high rangeland quality because of minimal livestock grazing (hereafter “sanctuary”), nested within the Ishaqbini Community Conservancy; (2) the Ishaqbini Community Conservancy (hereafter “conservancy”) with similarly high rangeland quality but in which large carnivores occurred; and (3) an area outside the community conservancy (hereafter “Ijara rangelands”) with similar numbers of large carnivores to the conservancy (Table S1), but lower rangeland quality (on account of high levels of livestock grazing that reduced forage availability). My study provides an example of how the tools of demographic analysis can be employed to guide reintroduction effort for a highly endangered species.

## **1.2 Materials and Methods**

### **1.2.1 Study area**

I conducted this work in Ijara (latitude: 1°36'33.95"S, Longitude: 40°32'35.43"E) and Fafi (latitude: 0°25'23.26"S, longitude: 40°13'46.42"E) sub-counties of Garissa County in eastern Kenya (Fig. 1A). Ijara is one of the driest regions in Kenya with an average annual rainfall ranging from 350-550 mm. These conditions are ideal for hirola, which thrive in open, semiarid grasslands (Kingdon 1982; Ali *et al.* in review). Livestock production was the most common land-use in the region and comprised goat (*Capra hircus*), sheep (*Ovis aries*), cattle (*Bos indicus*), camel (*Camelus dromedarius*), and donkey (*Equus asinus*) production. Large carnivores included lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyenas

(*Crocuta crocuta*), and African wild dogs (*Lycaon pictus*), which are common both in the conservancy and in the Ijara rangelands.

## **1.2.2 Demographic field study design**

### *1.2.2.1 Setting 1 (Sanctuary)*

In August 2012, a 25km<sup>2</sup> predator-proof sanctuary (latitude: 1°52'24. 94"S, longitude: 40°11'13. 55"E) was established within Ishaqbini Community Conservancy through a partnership between local communities, the Kenya Wildlife Service, and the Northern Rangelands Trust. The sanctuary had fence line posts with 5 m spacing and was 2.5 m tall. Electrified (6000-7000 V) strands of wires are spaced at 30 cm interval with wire mesh along the lower 1.5 m section, that extends 1m underground. Dedicated personnel, consisting of fence maintenance, fire control, and hirola monitoring teams patrol the sanctuary, on a daily basis. Prior to translocating hirola into the sanctuary, we removed livestock and large carnivores (6 spotted hyenas and 6 cheetahs), and established three permanent rain-catchment troughs. We then translocated 48 adult hirola (5 males, 39 females and 4 calves) from the outskirts of Ishaqbini Community Conservancy into the sanctuary using a combination of helicopter drives (n=12) and net-capture (n=24); additionally, 12 individuals were enclosed within the sanctuary at the time of construction. This sex and age composition approximated the social structure and densities reported for hirola groups throughout their geographic historical ranges (Andanje 2002). We immobilized net-captured individuals with a combination of 3 mg Etorphine hydrochloride (M99®; a narcotic) and 30 mg Azaperone (Stresnil®; a tranquilizer) with 6 mg Diprenorphine hydrochloride as a reversal. Prior to release, we fixed uniquely numbered ear tags on each individual to aid in subsequent identification and monitoring. These groups settled

into six distinct groups after the first six months and maintained this structure throughout the study period.

#### *1.2.2.2 Setting 2 (Conservancy)*

Located on the eastern bank of the Tana River and with an area of 215 km<sup>2</sup>, the Ishaqbini Community Conservancy (1°54'19.56"S, 40°12'49.89"E) was established in 2005 by Terra Nuova (an Italian non-government organization for conservation and rural development Njoroge *et al.* 2015). In an attempt to improve rangeland quality for hirola, livestock grazing has been minimized since 2008, thereby increasing grass abundance (Fig. S1). Approximately six hirola groups use the conservancy at varying times of the year. However, I restricted my analyses to 38 individuals in three resident groups that occupied the conservancy for the duration of my study. Hirola have stable groups and are faithful to particular areas, and I was able to identify individuals throughout the year using natural marks including ear nicks, horn size and shape, scars and coloration (Bro-Jørgensen & Durant 2003).

#### *1.2.2.3 Setting 3 (Ijara rangelands)*

From August 2012 to December 2012, we fitted GPS PLUS collars (Vectronic Aerospace, Germany) on nine adult females from seven different groups (mean group size =  $7.0 \pm 2.0$  SE, range = 5-11) in a 1000 km<sup>2</sup> area outside the conservancy and the sanctuary (Fig. 1A). This allowed us to relocate the seven groups once per month to estimate vital rates through resighting (Cormack 1964; Johnson *et al.* 2010). In collaring individuals, we followed the same capture procedures as the translocation effort. The Ijara rangelands were characterized by reduced grass abundance (stemming from high livestock grazing) and with comparable number

large carnivore to those of conservancy (Table S1). This setting is representative of the hirola's current and historical range. All procedures were conducted with a veterinary team under the authority of the Kenya Wildlife Service (KWS) and under permit number KWS/CRA/5001.

### **1.2.3 Demographic data collection and analysis**

I combined monthly ground surveys and weekly resightings of groups from all the three settings to estimate annual birth and survival rates (Johnson *et al.* 2010). During each survey, I identified all observed individuals and searched for any missing individuals that were counted in previous survey(s) for a period of up to two weeks. These were intensive bouts of searching, during which I covered over 7-12 km radius from where I detected the rest of the group. Following these counts, I interpreted any missing individuals as evidence of mortality. Further, I validated the number of individuals from first and second counts by dividing the observed counts against the verified counts to obtain the percent agreements. The mean agreements for three settings were 1) Sanctuary (97.6%), 2) Conservancy (89.8%), and 3) Ijara rangelands (87.7%, Table S2).

I used the Survival package in R version 3.2 (Therneau 2013) to generate mean survival rates for all the hirola age classes for three transitional years (2012-2015; Kaplan & Meier 1958; White & Garrott 1990). Subsequently, I used Popbio package in R version 3.2 (Stubben & Milligan 2007) to develop an age-structured matrix population model to project rates of population growth in each setting for three transitional years (2012-2015). In the implementation of the matrix model, I utilized the approach by Andanje (2002) to model hirola life history with three age classes (calves <1 year old, subadults  $\geq 1$  year -  $\leq 2$  years, and adults that are >2 years) to account for differences in survival and fecundity. With a life expectancy

of more than 10 years, female hirola give birth to a single calf at approximately three years. Following Caswell (2001), I constructed a female-based post-birth model with a one-year projection interval using a 3 x 3 matrix:

$$A = \begin{pmatrix} 0 & 0 & S_{ad} * F_{ad} \\ S_c & 0 & 0 \\ 0 & S_{sa} & S_{ad} \end{pmatrix} \begin{matrix} \text{calves} \\ \text{subadults} \\ \text{adults} \end{matrix}$$

where each matrix element represents a vital rate for each of the classes (calves, sub-adults and adults; Morris & Doak 2002) defined as  $S_c$  = survival rate for calves,  $S_{sa}$  = survival rate for subadults,  $S_{ad}$  = survival rate for adults and  $S * F_{ad}$  = fecundity rate for adult females. At the beginning of each census, I identified the proportion of individuals in each age class, and matched these with corresponding survival and fecundity rates. Similar to other alcelaphine antelopes, the majority of females (>50%) exhibit a birth pulse at the beginning of the short rains in October-November although breeding can occur throughout the year (Rutberg 1987; Andanje 2002). Therefore, I used a post-breeding census to estimate adult fecundity, measured as the averaged proportion of adult females with calves within 12 months. I assumed a 50:50 sex ratio for all calving (I could not distinguish sexes of calves) in estimating female fecundities. Hirola have an eight-month gestation period and I observed calves for 97% of pregnant females. I did not note any instances of abortion or resorbtion.

With a post-breeding census approach, non-zero matrix elements in the top row of the matrix represent the product of adult fecundity and survival. From the matrix, I estimated the population growth rate ( $\lambda$ ) as the dominant eigenvalue (Caswell 2001) and calculated the geometric means for each setting. Similarly, I calculated both analytical sensitivity and elasticity estimates for different vital rates across each setting. I conducted a Life Table

Response Experiment to decompose treatment effects on  $\lambda$  into contributions from setting specific vital rates (Wisdom, Mills & Doak 2000; Bruna & Oli 2005; Barclay, Korfanta & Kauffman 2011). LTRE analysis quantifies the contributions of variation in vital rates to variations in  $\lambda$  from control and treatment populations (Horvitz, Schemske & Caswell 1997). LTRE contributions were calculated from a matrix model for the 2012–2015 period using averaged vital rates estimated from each population to facilitate pairwise comparisons (sanctuary vs conservancy; sanctuary vs Ijara rangelands; conservancy vs Ijara rangelands). I calculated the change in  $\lambda$  between each paired setting as  $\Delta\lambda = \lambda_i - \lambda_j$  which can also be estimated

using: 
$$\sum_m (v_{m_i} - v_{m_j}) * s_{ij}$$

Where,  $(v_{m_i} - v_{m_j}) * s_{ij}$  is the difference in the vital rate  $m$  for the paired settings, and  $s_{ij}$  the mean sensitivity derived from the vital rates averaged over the study period. For the LTRE contributions from each year, I calculated the percentages over the study period by dividing the term by  $\Delta\lambda$ .

### 1.3 Results

Mean survival rates between the three age classes differed across the settings, with adult survival consistently higher (0.65-0.95  $\pm$ 0.038SE) than sub-adult (0.58-0.95 $\pm$ 0.11SE) and calf survival (0.47-0.93 $\pm$ 0.069SE), and survival rates for all three ages were highest in the sanctuary (Fig. 2). Of particular note were (1) increases in calf survival due to large carnivore exclusion ( $S_c$  sanctuary >  $S_c$  conservancy  $\approx$   $S_c$  Ijara rangelands); (2) increases in sub-adult survival due to predator exclusion ( $S_{sa}$  sanctuary >  $S_{sa}$  conservancy  $\approx$   $S_{sa}$  Ijara rangelands); and (3) increases in adult survival due to heightened rangeland quality ( $S_{ad}$  sanctuary  $\approx$   $S_{ad}$  conservancy >  $S_{ad}$  Ijara rangelands). Adult survival elasticity was markedly higher in the conservancy and Ijara

rangelands compared to the elasticity in the sanctuary (Table 2). The mean elasticity estimates for the sub-adult and calf survival remained constant within settings (2012–2015), while adult fecundity showed low sensitivity and varied little between the settings (Table 2).

Population growth rates ( $\lambda$ ) of hirola were highest in the sanctuary ( $1.08 \pm 0.03$  SEM, followed by the conservancy ( $0.95 \pm 0.07$  SEM), and the outlying rangelands ( $0.86 \pm 0.08$  SEM; Fig. 3). Adult survival, fecundity and calf survival were the primary contributors to bolstered population growth following large carnivore exclusion (Fig. 4A), whereas adult survival was the primary contributor to increased population growth stemming from differences in rangeland quality (Fig. 4B, C).

#### **1.4 Discussion**

By utilizing a large-scale, large carnivore exclosure and capitalizing on natural variation in rangeland quality, I quantified demographic drivers for the critically endangered hirola antelope in eastern Kenya. Since the 1970s, populations of hirola have been declining with a marked dip in numbers due to a rinderpest (*Morbillivirus*) outbreak in 1985 (Fig. 1B; Andanje 2002). Nevertheless, and despite the eradication of rinderpest from Kenya in 2001 (Mariner *et al.* 2011), hirola populations have never recovered to pre-crash levels. My findings show that vital rates varied across the different settings, where for example, survival of adults differed across settings - highest in the sanctuary and lowest in Ijara rangelands (Fig 2). The higher variability in survival of calves and sub-adults compared to adults conforms with demographic buffering in other ungulates across the globe (Gaillard, Festa-Bianchet & Yoccoz 1998; Raithel, Kauffman & Pletscher 2007; Bjørkvoll *et al.* 2015).



Population growth rates estimates in the three settings suggested a declining trend from the sanctuary (in which  $\lambda > 1$ ) to the conservancy ( $\lambda \approx 1$ ) and the outlying rangelands ( $\lambda < 1$ ; Fig 3). I interpret differences in population growth between the sanctuary and conservancy to be due to predation, which may cause differences in fecundity and calf survival (Fig. 4). Differences in population growth between the sanctuary and outlying rangelands were sufficient to shift population growth from stable to negative attributable to differences in rangeland quality. Overall, both low livestock densities and the associated increase in rangeland quality or the exclusion of large carnivores, lead to positive population growth. Consequently, this results suggest that hirola are able to contend either with low rangeland quality or predation, but not to the simultaneous effect of both. The combined effects of reduction in rangeland quality or predation are likely responsible for the inability of hirola to recover. While there are few long-term studies that have focused on tropical systems, ungulates in African savanna can show marked temporal variations (Sinclair 1983; Owen-Smith & Mason 2005). These population fluctuations are associated either with (1) spatial heterogeneity in rangeland quality and (2) heightened predation due to poor habitat conditions (Mduma, Sinclair & Hilborn 1999; Sinclair, Mduma & Brashares 2003; Owen-Smith & Mason 2005; Grange *et al.* 2015). It is therefore often difficult to assess the relative roles of predation and rangeland quality in driving population declines, which are often exacerbated by both stochastic environmental variation and density dependent factors. Elsewhere, reduced fecundity among adults has been reported to occur when juvenile survival declined substantially (Eberhardt 2002; Ogutu, Piepho & Dublin 2014; Grange *et al.* 2015).

In the vast rangelands of eastern Kenya, hirola declines can partly be associated with reduced rangeland quality, mostly stemming from overgrazing, fire suppression and

megaherbivore extirpations (Ali *et al.* in review). Similarly, and over a comparable period, cattle that co-occurred with hirola experienced a 74% declines, while there is no evidence that large carnivore numbers have changed within hirola historical ranges (Ali *et al.* in review). My findings demonstrate the importance of changes in adult survival stemming from declining rangeland quality in determining population dynamics of a critically endangered ungulate. These observations are consistent with other studies that have shown the variations in adult survival and thus the lack of paradigm in the survival of tropical ungulates (Owen-Smith & Mason 2005). However, my finding equally reinforces the importance of calf survival and adult fecundity in contributing to ungulate population dynamics reported for temperate ungulates (Gaillard, Festa-Bianchet & Yoccoz 1998; Raithel, Kauffman & Pletscher 2007).

In conclusion, my results provide improved estimates of hirola vital rates and their association with environmental factors; these findings can be used to guide future hirola reintroduction efforts. Population growth rates were mainly driven by fecundity and calf survival following large carnivore exclusion, whereas adult survival was the primary contributor to differences in population growth that stemmed from differences in rangeland quality. The future of hirola as a species depends on Ijara rangelands, which have experienced the expansive conversion of high-quality rangelands (grasslands) to tree cover. In this regard therefore, I recommend a primary strategy of rangeland restoration to enhance the survival and fecundity of adult females.

## **1.6 References**

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## Tables

**Table 1:** Mean difference in survival rates, adult fecundity and sensitivities for age classes between pairs of settings, from 2012 – 2015 study period.

<b>Age class</b>	<b>Sanctuary vs Conservancy</b>	<b>Sanctuary vs Ijara rangelands</b>	<b>Conservancy vs Ijara rangelands</b>	<b>Sanctuary vs Conservancy</b>	<b>Sanctuary vs Ijara rangelands</b>	<b>Conservancy vs Ijara rangelands</b>
	Mean change in survival and range			Mean sensitivity and range		
<b>Calf</b>	0.368 (0.20-0.6)	0.458 (0.19-0.80)	0.090 (0.02-0.16)	0.09 (0.08 -0.10)	0.09 (0.07-0.11)	0.07 (0.03-0.09)
<b>Sub-adult</b>	0.327 (0.03-0.7)	0.365 (0.20-0.60)	0.038 (-0.10-0.17)	0.09 (0.07-0.10)	0.09 (0.06-0.10)	0.06 (0.02-0.09)
<b>Adult</b>	0.041 (0.01-0.1)	0.295 (0.10-0.63)	0.254 (0.11-0.53)	0.86 (0.84-0.89)	0.86 (0.83-0.90)	0.91 (0.86-0.98)
<b>Fecundity</b>	0.056 (0.05-0.1)	0.084 (0.02-0.12)	0.027 (-0.03-0.06)	0.47 (0.38-0.58)	0.47 (0.36-0.57)	0.34 (0.08-0.54)

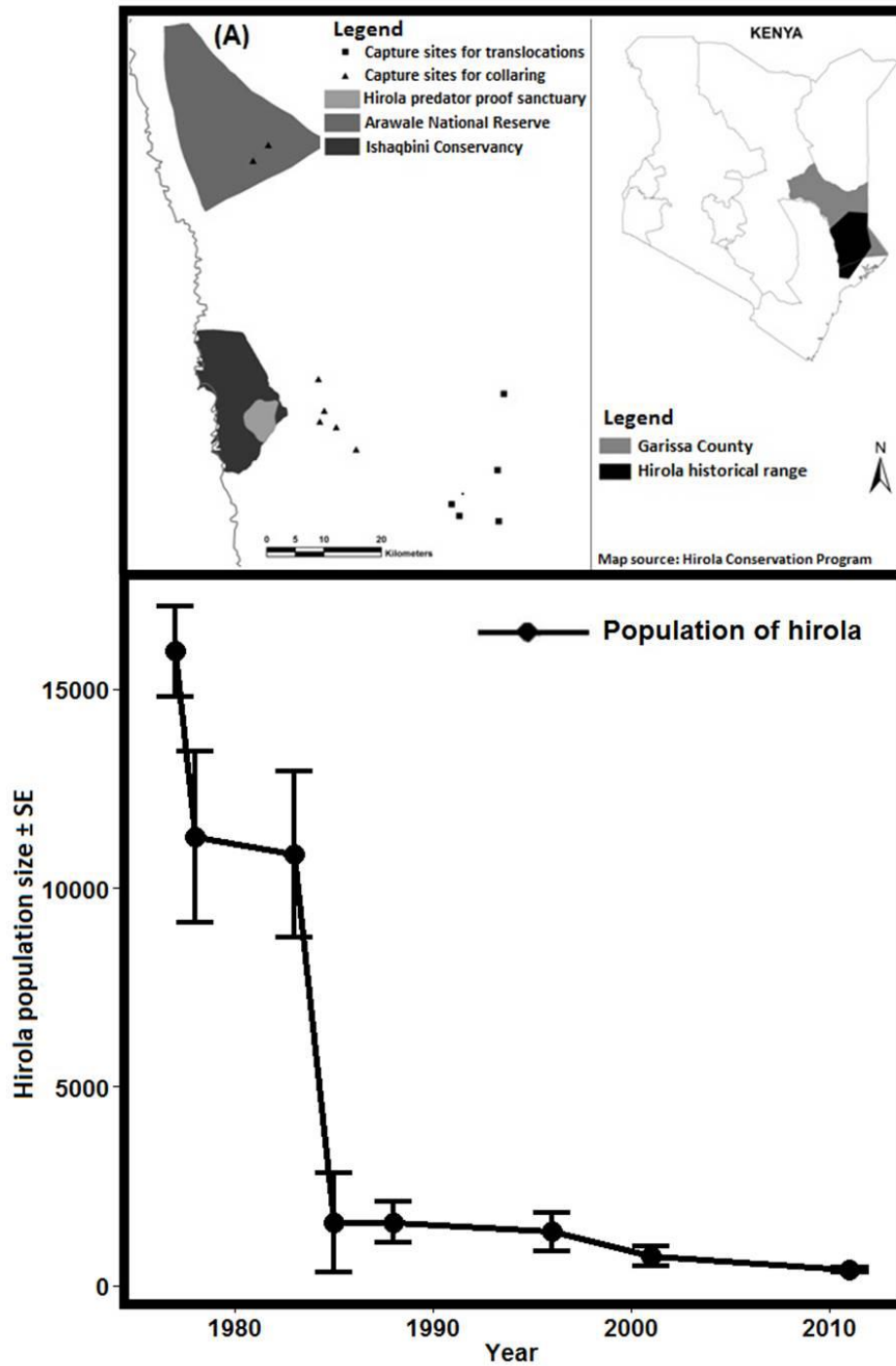
**Table 2:** Elasticity estimates for calves, sub-adults and adults.

<b>Setting</b>	<b>Calf Elasticity</b>	<b>Sub-adult Elasticity</b>	<b>Adult Elasticity</b>
<b>Sanctuary</b>	0.099	0.099	0.703
<b>Conservancy</b>	0.426	0.426	0.872
<b>Ijara rangelands</b>	0.043	0.043	0.869

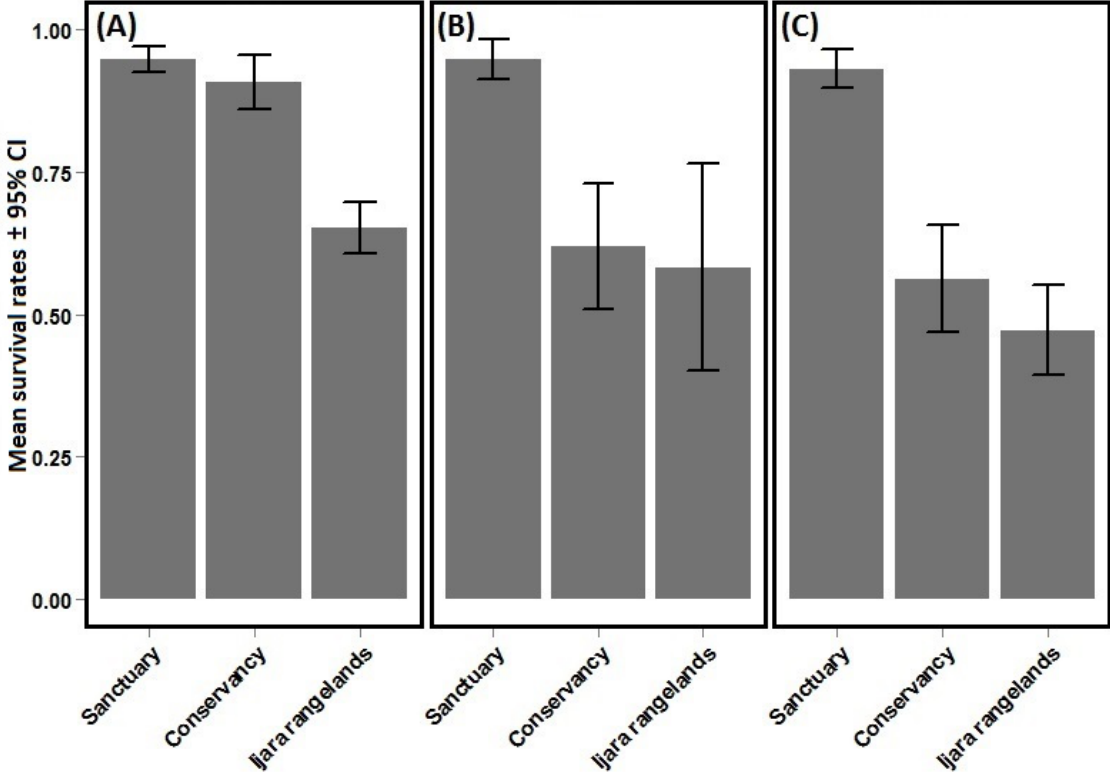


## Figures

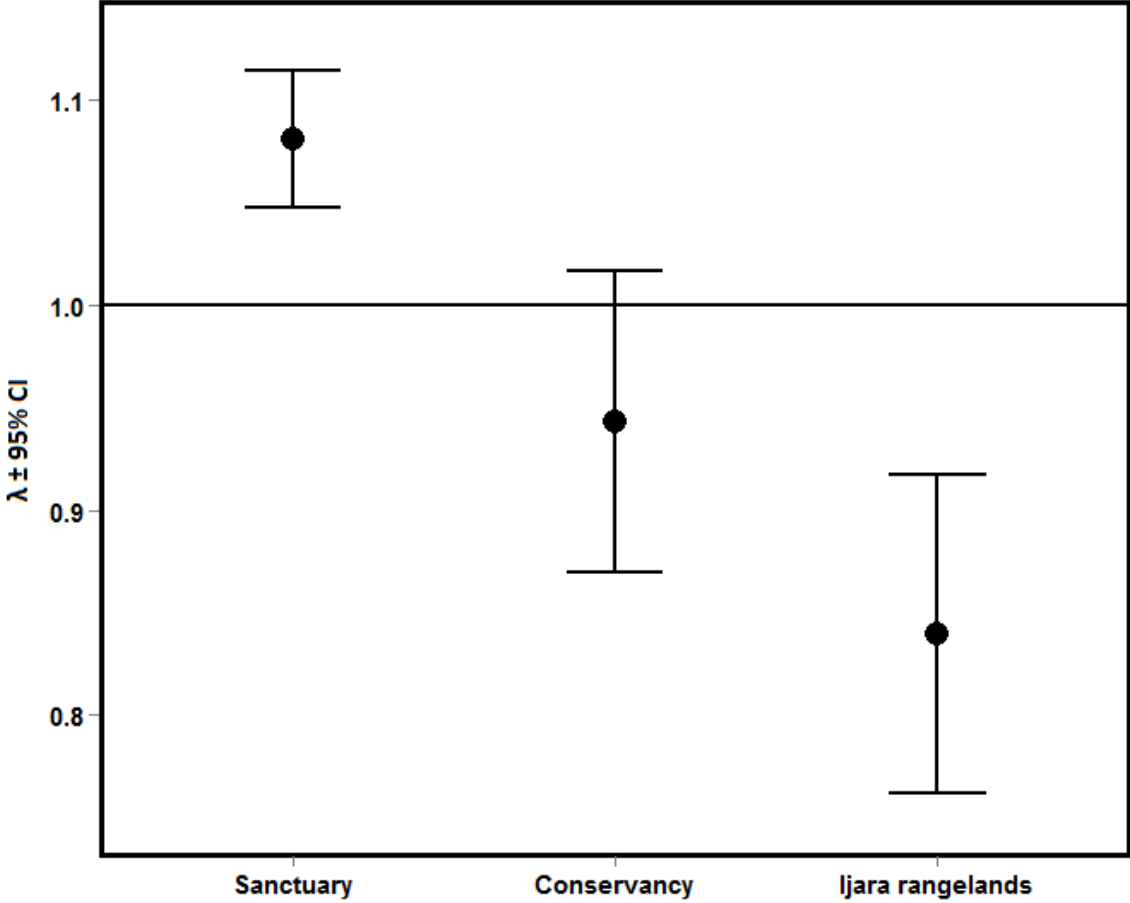
**Figure 1:** (A) Map of Kenya and the study area in Garissa County, Kenya and (B) Estimated hirola population trends from 1977 – 2011, Data courtesy of the Kenya Department of Resource Surveys and Remote Sensing.



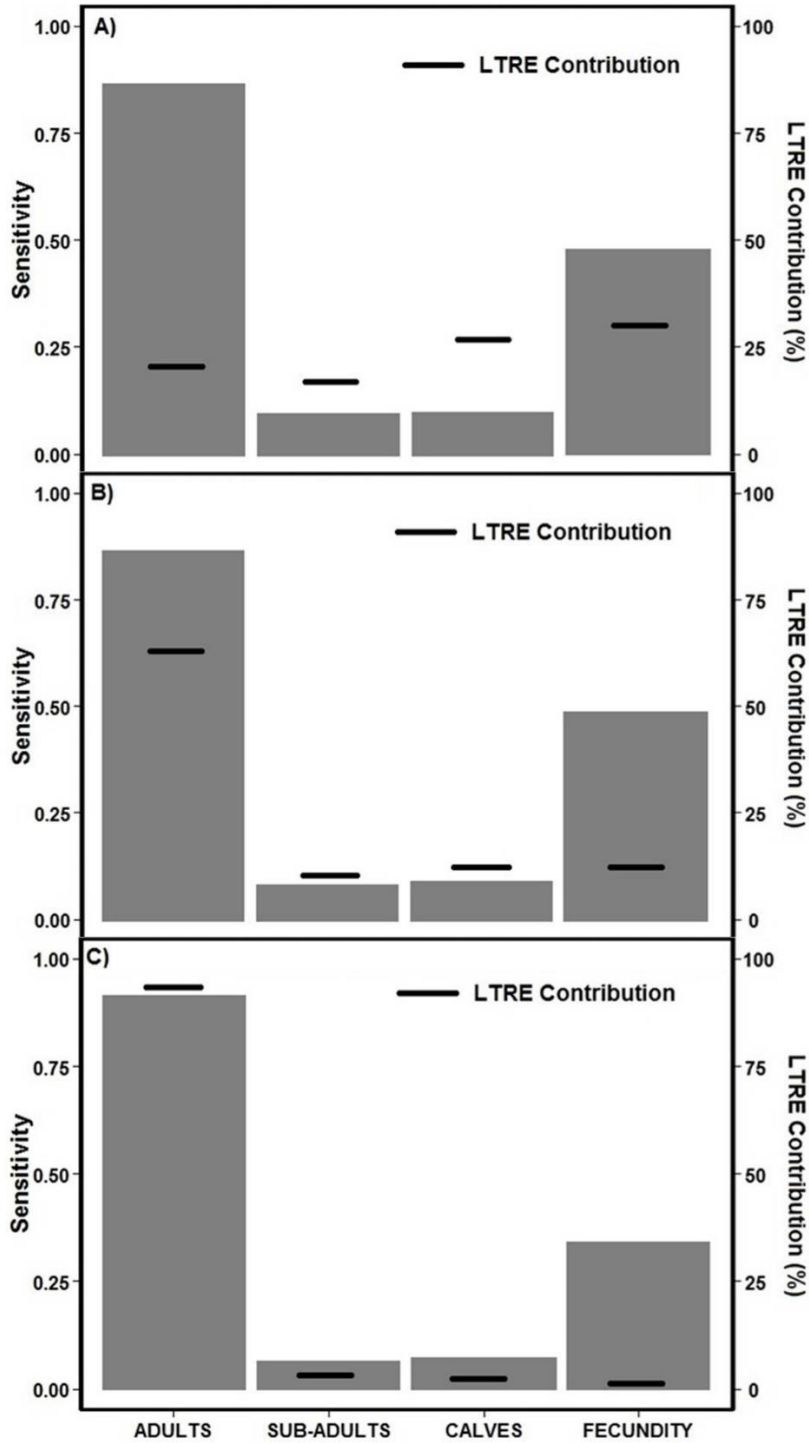
**Figure 2:** Mean survival rates ( $\pm$  95% CI) for hirola in the sanctuary, conservancy and Ijara rangelands for (A) adult, (B) sub-adult and (C) calf on the 2012 – 2015 study period.



**Figure 3:** Long term growth rates ( $\lambda$ ;  $\pm$  95% CI) of hirola in the sanctuary, conservancy, and the Ijara rangelands based on the 2012 – 2015 study period.



**Figure 4:** Results from a life table response experiment (LTRE) indicating the sensitivity and percent contributions of vital rates for 2012 – 2015 to the population growth changes in hirola for paired settings A) sanctuary vs conservancy, B) sanctuary vs outlying areas (Ijara rangelands) and C) conservancy vs outlying areas (Ijara rangelands).



## Chapter 2

### **Resource selection and landscape change reveal mechanisms underlying range collapse for the world's most endangered antelope**

#### **2.1 Introduction**

The decisions by which animals select and utilize resources are ubiquitous mechanisms for maximizing fitness. Resource selection links the behaviour of individuals to a host of broader population-level phenomena, including the relative strength of top-down and bottom-up control of populations, and the distribution of species across landscapes (Manly *et al.* 2002; Bowler & Benton 2005; Calcagno *et al.* 2011; Thaler, McArt & Kaplan 2012; Landman & Kerley 2014; Doherty *et al.* 2015; Terborgh 2015). Consequently, understanding resource selection for species or populations of conservation concern can inform recovery efforts, the design of protected areas, and predicted responses of animals to human disturbances (Martin 2001; Johnson, Seip & Boyce 2004; Cañadas *et al.* 2005; Sawyer & Kauffman 2011; Selwood, McGeoch & MacNally 2014).

Human disturbance can constrain the distribution of populations across landscapes and, in extreme instances, trigger geographic range collapse of entire species (Laliberte & Ripple 2004; Kummerle *et al.* 2012; Ogada *et al.* 2015). These broad-scale patterns often are rooted in habitat loss, which affects resource selection through at least two pathways: demography and individual movements. Additionally, habitat loss can influence resource selection and subsequent range collapse directly (i.e., through reductions in food or birth sites (Sutherland 1996)), or indirectly by increasing predation risk or poaching pressure (Wittmer, Sinclair & McLellan 2005; DeCesare *et al.* 2010). For example, woodland caribou (*Rangifer tarandus*

*caribou*) are thought to have declined in western Canada because an influx of moose (*Alces alces*) into clear-cut areas subsidizes an elevated number and hunting efficiency of predators, thereby resulting in apparent competition (Wittmer, Sinclair & McLellan 2005). Similarly, and in East Africa, impala (*Aepyceros melampus*) avoid risky (high-tree cover) areas where predators hunt. As a result, most impala consume plants with low palatability that dominate safe areas, whereas more palatable forage is avoided because it tends to occur in risky areas (Ford *et al.* 2014).

In African savannas, tree cover is regulated by a combination of fire, precipitation, and herbivory (Scholes & Archer 1997; Sankaran *et al.* 2005; Anderson & Hoffman 2007; Riginos & Grace 2008; Moe *et al.* 2009; Devine *et al.* 2015). Both experimental and observational studies demonstrate that tree cover increases following large-herbivore extirpation or removal (Van De Vijver, Foley & Olf 1999; Augustine & McNaughton 2004; Goheen *et al.* 2013; Daskin, Stalmans & Pringle 2016). In addition, tree encroachment has been associated with reduced competition from grasses stemming from overgrazing (Eckhardt, Wilgen & Biggs 2000; Riginos 2010).

As the world's most endangered antelope, the hirola (*Beatragus hunteri*) has been declining since the 1970s (IUCN 2008; Probert *et al.* 2014). Hirola are reported to be pure grazers (Kingdon 1982) and, in historical times, occurred throughout open grasslands along the Kenya-Somalia border (eastern Kenya and southwestern Somalia). While the underlying mechanisms are unclear, some combination of loss of grassland habitat and predation are thought to underlie low abundances and geographic-range contraction of contemporary populations (Andanje 2002; Kock *et al.* 2006). Although a rinderpest (*Morbillivirus*) outbreak in the mid-1980s led to mass mortality of hirola and other ruminants across eastern Kenya, its

eradication by 2001 (or even earlier within the hirola's historical range; Mariner *et al.* 2012) did not prompt the subsequent recovery of hirola. Consequently, major questions remain as to why hirola have not rebounded in the three decades since rinderpest eradication.

To elucidate the factors underlying chronic low numbers of hirola, I sought to link contemporary resource selection of hirola with potential drivers of range collapse. I addressed the following questions: (1) have hirola populations experienced habitat loss via tree encroachment since rinderpest eradication? and (2) if tree encroachment has occurred, has this resulted in intensified predation pressure on hirola?

## **2.2 Methods**

### **2.2.1 Study area**

I conducted work in the historical geographic range of hirola in Garissa County, Kenya, 0° 25'S, 40° 32'E and ~80m A.S.L. (Fig 1A). This area is semi-arid (annual rainfall = 350-500 mm; Bunderson 1979, 1981), with rainfall occurring in two distinct seasons. The long rains—locally known as “Guu”—occur in April to June, and the short rains—or “Deir”—occur in November to December. Similarly, there are two distinct dry periods: the short dry season (January-March) and the long dry season (July-October). The average annual temperature is 30°C, and it can exceed 36°C during dry seasons.

In Kenya, the historical geographic range of hirola covered ~17,000 km<sup>2</sup> in southern Garissa County, the majority of which is inhabited by Somali pastoralists who subsist on goats (*Capra hircus*), sheep (*Ovis aries*), camels (*Camelus dromedarius*), and cattle (*Bos indicus*). According to the 2009 national census, 17 million livestock are estimated to occur in the entire northeastern region of Kenya (Garissa, Mandera, and Wajir counties; Republic of Kenya 2010).

My study area falls within the Greater Horn of Africa biodiversity hotspot; here, conservation for a multitude of endemic species is hampered by civil unrest and poor infrastructure (Hanson *et al.* 2009; Mariner *et al.* 2012; Amin *et al.* 2015). The most common ungulates in the area include the reticulated giraffe (*Giraffa camelopardalis reticulata*), gerenuk (*Litocranius walleri*), lesser kudu (*Tragelaphus imberbis*), waterbuck (*Kobus ellipsyprimnus*), and Kirk's dik-dik (*Madoqua kirkii*). Large carnivores in the region include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), and African wild dogs (*Lycaon pictus*).

## **2.2.2 Data collection and analysis**

### *2.2.2.1 Quantifying tree encroachment within the hirola's historical range*

To quantify the changes in tree cover within the hirola's historical geographic range, I classified two remotely-sensed images acquired in 1985 (Landsat 5) and 2012 (Landsat ETM+7). Specifically, I used images taken during the dry season to distinguish understory vegetation from tree cover. I estimated the extent of the hirola's historical range based on the earliest recorded distribution of hirola, in which over 90% of the study area fell within a single Landsat scene (path 166 row 65). I performed a random forest classification (Breiman 2001) using the package Random Forest in R version 3.2 (Liaw & Wiener 2012; R Development Core Team 2014). I classified each pixel from each image as tree cover, non-tree cover, cloud and shadow areas. Random Forest is a bootstrap classification and regression tree (De'ath & Fabricius 2000; Evans & Cushman 2009) where an ensemble of weak-learners are used to make an optimal estimate based on a fit to the data. The method is robust to noise and autocorrelation (Breiman 2001; Hastie, Tibshirani & Friedman 2009). Random Forest validates against the data withheld



in a given bootstrap, thus negating the need for an independent data withhold. As such, a robust measure of model fit is reported.

For ETM+7 images that exhibited the scan-alignment issue (acquired after May 2003), I applied a gap-filling algorithm in ENVI 5.0 (Chen *et al.* 2011). To train the model, I digitized a minimum of 100 observations for each image. The model was specified with 1001 bootstrap replicates. Each image was classified in a separate model and the four classes predicted using the raster package in R version 3.2 (Hijmans & Van Etten 2012). For each classified image, I reclassified clouds and shadows into “no data” using ArcGIS, such that I was left with two classes in the image: tree cover and non-tree cover. Given the abundance of cloud cover over the study area through time, I combined multiple images (Table S1) for each time step, to iteratively fill in the “no data” classes created by cloud and shadow. Each of the two time steps (1985 and 2012) required four images to account for cloud cover. This allowed me to develop a single cloud-free image in which I filled missing data with values from corresponding images with a similar acquisition date (Wijedasa *et al.* 2012). To validate the model fit, I used Out-Of-Bag error (OOB; Fawcett 2006; Evans & Cushman 2009). Over a comparable period (1977-2011) to that elapsed between image classification, abundances of hirola and other herbivores occurring in the hirola’s historical geographic range were assessed by aerial transects flown by the Kenya Department of Resource Surveys and Remote Sensing (DRSRS 1977-2011; Fig. S1).

#### 2.2.2.2 *Hirola capture and collaring*

For three months prior to hirola captures (May-July 2012), and with the support of field collaborators, we monitored the locations and the movements of hirola herds from field

vehicles and on foot to minimize search time in the subsequent collaring process. Between August-December 2012, we immobilized nine adult females from seven herds (mean herd size =  $7.0 \pm 2.0$  SE, range = 5-11) from a Bell 206 helicopter. To minimize capture induced hyperthermia and exposure, we conducted all captures between 0600-0800 hours. We descended within 1015 m above the ground, and fired 0.22 calibre blanks to propel a metal syringe and deliver 3 mg Etorphine hydrochloride (M99®; a narcotic) into the hind muscle of adult females (75-85 kg). Following darting, our three-person team descended on and blindfolded individuals. We injected 30 mg Azaperone (Stresnil®; a tranquilizer) intravenously to increase depth of sedation and minimize stress on the captured individuals. During anaesthesia, we kept hirola in sternal recumbence to prevent bloating and regurgitation. We marked each individual with a uniquely numbered ear-tag and fitted each individual with a GPS satellite collar set to collect and transmit hourly fixes (995 g, circumference of 47 cm; Vectronic Aerospace, Germany) before using 6 mg Diprenorphine hydrochloride as a reversal agent. Within two minutes of administering the reversal agent, individuals exhibited regular movements (walking, running) and rejoined with their herds. All procedures were conducted with a veterinary team under the authority of the Kenya Wildlife Service and under permit number KWS/CRA/5001. By fitting hirola with GPS collars, we (1) relocated and re-sighted the nine individuals along with their respective herds once per month; and (2) assessed resource selection and movements of hirola herds. While we collared a total of nine individuals, two herds contained two collared females giving a total of seven distinct herds for tracking. Collectively, these herds contained 54 individuals, or roughly 13.5% of the global population (King et al. 2011). Because hirola herds are cohesive (Kingdon 1982), I interpreted the individual movements as indicative of movements of the entire herd.

### 2.2.2.3 Development of step selection functions (SSFs)

I collected hourly GPS fixes from individuals (and movements of their associated herds) from August 2012 to October 2015. To model resource selection, I used a step-selection function (hereafter referred to as “SSF”) and created series of “clusters” (10 random steps based on the empirical distribution of turning angles and step lengths (Fortin *et al.* 2005)) that then were associated with each observed step. I tested for selection of five landscape variables: tree cover (binary), landscape curvature (a metric of topographic relief; Anderson *et al.* 2010), distance to road, distance to permanent water (rivers and streams), and distance to village.

I used the individual animal and cluster (i.e., the observed step and its 10 associated random steps) as nested random effects. Step-selection functions use segments of a landscape (not individual locations) as sampling units. The SSF models do not assume that an animal moved along the straight-line path between two successive points, but instead quantify resource selection in areas available to the animal (Fortin *et al.* 2005; Coulon *et al.* 2008). I developed separate models for day and night, and for wet and dry seasons. Resource selection of ungulates has been shown to shift seasonally (Godvik *et al.* 2009), and I also suspected that shifts in resource selection might occur throughout the day because (1) predators are most active at night; (2) humans are least active at night; and (3) thermal stress is lowest at night. I used model selection procedures to determine which landscape variable or combination of landscape variables best predicted habitat selection. I used AIC to rank models (Burnham & Anderson 2002), and present averaged coefficients for models  $\Delta AICc < 4$  (Tables S2 and S3).

#### 2.2.2.4 Link between tree encroachment and habitat loss

Because increasing tree cover could be associated with both greater predation risk (Ford *et al.* 2014; Hopcraft, Sinclair & Packer 2005; Riginos 2014) and lack of forage for grazers like hirola (du Toit & Cumming 1999; Riginos 2010), I compared tree cover in current (2012; ca. 1000 km<sup>2</sup>) and historical (1985; ca. 17,000 km<sup>2</sup>) geographic ranges of hirola. If tree cover has increased during the period of hirola decline, it may be indicative of habitat loss. However, I have no *a priori* knowledge of how much tree cover is ‘too much’ for hirola at the scale of an individual’s home range, so simply observing a change in tree cover would not allow to quantify habitat loss. Moreover, because of their small population size, there may be unoccupied areas of suitable habitat outside of the current distribution of hirola that could serve as future reintroduction sites. Thus, I quantified the amount of tree-cover change in areas equivalent in size and shape to those of an average hirola home range (hereafter referred to as ‘potential home ranges’) within the current and historical geographic ranges. I estimated the number of potential home ranges containing less than or equal to the amount of tree cover within observed home ranges. The amount of tree cover observed in wet season home ranges ( $54\% \pm 14\%$  SEM,  $n = 7$ ) was similar to that observed in dry season home ranges ( $58\% \pm 12\%$  SEM,  $n = 7$ ).

To estimate home-range sizes (Table 1) and shapes, I quantified the 95% isopleths of the utilization distribution from the seven GPS-collared individuals associated with independent herds using the tracking data from 2012-15. To create the utilization distributions, I used a kernel density estimator with a least-squares cross validation smoother. All home ranges exhibited a similar rectangular shape, with the long axis running along a north-south gradient at  $\sim 110^\circ \pm 18^\circ$ . The mean dimensions of wet season home ranges (width =  $3858 \text{ m} \pm$

342 m SEM; length = 10,505 m  $\pm$  1466 m SEM) were smaller than dry season home ranges (width = 4461 m  $\pm$  972 m SEM; length = 13,743 m  $\pm$  2854 m SEM). Using these dimensions, I created potential home ranges by superimposing two grids on the historical geographic range of hirola, with the cell size of each grid matching the season-specific home range dimensions. These grids resulted in 228 dry season potential home ranges and 361 wet season potential home ranges within the historical geographic range of hirola. I calculated the total amount of tree cover within each potential home range, and determined if this amount exceeded the seasonal means for tree cover observed within actual hirola home ranges. I then used a paired *t*-test to test for differences in tree cover between 1985 and 2012, replicated over the potential home ranges.

#### *2.2.2.5 Link between tree encroachment, predation, and movements*

Although I lacked data to test an exhaustive list of mechanisms underlying the correlation between tree cover and hirola abundance, I did test the hypothesis that predation pressure—and thus mortality of hirola—had increased with tree encroachment. Between 2007 and 2015, a network of local scouts opportunistically recorded the locations of sites where hirola were killed (hereafter “kill sites”) using handheld GPS units. Hirola scouts identified kill sites on foot or from a vehicle to identify hirola carcasses in both open and tree cover areas. Over this nine-year period, 59 kill sites were discovered and assigned a predator identity based on tracks, fur removal, and bite marks at the kill site (Ford *et al.* 2014). These kills were made by lions (39%), cheetahs (25%), African wild dogs (12%), and other (i.e., unidentified; 24%).

I constructed a resource selection function (RSF) for kill sites based on the same five landscape variables used as predictors in the SSF. Here, the RSF quantifies the probability of

occurrence of a kill site relative to the five landscape variables. For tree cover and landscape curvature, a positive RSF coefficient indicates a higher than expected chance that a sample location will be an observed kill site compared to a random location. For distance to roads, rivers, and villages, a negative RSF coefficient means that proximity to these features increases risk of predation. To create the RSF, I constructed a minimum convex polygon (MCP) around all combined kill sites and used GIS software to sample an equal number of random locations ( $n = 59$ ) within the MCP. I then used logistic regression (1 = observed, 0 = available) to estimate RSF coefficients (Manly *et al.* 2002). I used AIC to rank kill site RSF models, and present averaged coefficients for models  $\Delta AICc < 4$  (Table S4).

Because the distribution of hirola inevitably constrains the distribution of kill sites, I also calculated the *per capita* risk of mortality from predation (PCR; *sensu* Ford *et al.* 2014). PCR is a ratio of the number of kill sites found in a given habitat (e.g., tree cover) to the proportion of GPS fixes observed within that same habitat. When  $PCR \approx 1$ , kill sites occur in proportion to the amount of time live animals spend in that habitat. Values  $< 1$  indicate the habitat is relatively safe, while values  $> 1$  indicate that the habitat is relatively risky. If  $PCR > 1$  for tree cover, and tree cover has increased since 1985, predation risk may have also increased for hirola. I acknowledge that kill sites may be more difficult to detect in tree cover and the relationship between PCR and tree cover may be an underestimation (although I would not expect such underestimation to vary systematically between 1985 and 2012). According to the Kenya Wildlife Service, there is no evidence that the abundance of large carnivores has changed directionally between 1985 and 2012 in the study area (C. Musyoki, personal communication).

### 2.3 Results

Within the historical geographic range of hirola, and following the rinderpest outbreak of 1985, tree cover increased by 251% between 1985 and 2012 (Fig.1). In the wet season, 74% of potential home ranges ( $n = 267$ ) had equal or less tree cover in 1985 than currently-occupied home ranges, while only 26% of potential home ranges had this amount of tree cover or more in 2012. Similarly, in the dry season, 79% of potential home ranges ( $n = 59$ ) had equal or less tree cover in 1985 than currently-occupied home ranges, while only 32% of potential home ranges had this amount of tree cover in 2012. Thus, tree cover has increased significantly between 1985 and 2012 ( $p < 0.0001$ ), resulting in the loss of 43-53% of suitable, potential home ranges.

Step-selection functions demonstrated that hirola consistently avoided tree cover in all seasons (wet and dry) and times (day and night; (Fig. 2A and 2B)). Results of the kill-site RSF suggest that kill sites were more likely to occur near villages, near roads, and in areas with highly convex curvature (Fig. 3). Tree cover was not a strong predictor of kill site occurrence. Similarly, the average *per capita* risk of mortality was slightly higher—though statistically indistinguishable—in open areas compared to areas near tree cover (Fig. 3 inset). In other words, tree cover was not riskier for hirola than open areas.

### 2.4 Discussion

I quantified habitat loss and resource selection for hirola in eastern Kenya to elucidate the factors underlying population declines of hirola. My findings indicate that there was a 251% increase in tree cover between 1985 and 2012, strongly suggesting that historical range collapse and contemporary low numbers of hirola are due largely to habitat loss via tree encroachment.

Why did tree cover increase so markedly over the past three decades? I entertain three possible, non-exclusive scenarios. First, overgrazing by livestock may have reduced grasslands and increased tree cover (du Toit & Cumming 1999). The Kenya Department of Resource Surveys and Remote Sensing has documented an increase in goats, camels, and sheep coincident with a decline in cattle, over the course of time during which tree encroachment occurred (Fig. S1). In the rangelands of eastern Kenya, most land is utilized for livestock production by nomadic communities. Gradually, however, sedentary pastoralism is becoming more common, increasing grazing pressure. As trees encroached at the expense of grasslands throughout the historical range of hirola, most pastoralists have shifted from grass-dependent cattle to browsing livestock such as goats and camels (Fig. S1; see also Kassahun, Snyman & Smit 2008). This pattern is congruent with my interpretation that lack of recovery of hirola populations and sustained low production of cattle are rooted in the loss of grasslands on which both wild and domestic grazing ungulates rely.

Second, elephant extirpation may have fuelled tree encroachment and subsequent reduction of grasslands. Elephants browse, uproot, and kill trees, thereby reducing tree cover in many African savannas (Owen-Smith 1989; Baxter & Getz 2005; Morrison, Holdo & Anderson 2015; Daskin, Stalmans, & Pringle 2016). Consequently, hirola could be exhibiting a secondary extinction debt (*sensu* Brodie *et al.* 2014) in which tree encroachment stemming from elephant extirpation has triggered the dramatic decline of the world's most endangered antelope. Third, fire suppression in sub-Saharan Africa may have led to tree encroachment (Baxter & Getz 2005). As was the case elsewhere in sub-Saharan Africa, traditional use of fire in eastern Kenya was discouraged by the government in the 1970s. Additionally, road construction by petroleum companies in the 1970s in Garissa County may have facilitated fire



breaks that eventually curbed the use of fire altogether (Ali Diis, Ministry of Livestock, Kenya, personal communication).

My kill-site analyses strengthen the interpretation that tree encroachment has impacted hirola primarily via loss of forage, as tree cover was a poor predictor of kill sites. Similarly, the *per capita* risk of mortality did not differ as a function of tree cover, suggesting that tree encroachment is influencing hirola populations primarily through bottom-up pathways. While lions were the most frequent predators of hirola in my study area, other large carnivore populations in Garissa County (cheetahs and wild dogs) may collectively suppress contemporary hirola recovery. Although I lack data on predator abundance, a close relative of hirola in my study area (the coastal topi, *Damaliscus lunatus* ssp. *topi*) exhibited comparable declines to those of hirola in the 1980s but has since rebounded. This suggests that predation on topi has not increased over time, and I expect similar levels of predation on both topi and hirola. However, unlike hirola, the dry season range for topi extends into the moist coastal forests in eastern Kenya, which may buffer them from loss of forage due to tree encroachment. In light of the three scenarios detailed above, I find little support that tree encroachment has made hirola more vulnerable to predation, and that hirola seem to avoid tree cover primarily because of lack of forage.

I conclude that some combination of overgrazing, elephant extirpation, and fire suppression drove tree encroachment, and this tree encroachment has impeded hirola recovery following rinderpest eradication. My work provides justification to national agencies and nongovernment organizations to integrate rangeland restoration with hirola-conservation efforts. Range restoration will be most successful, however, when it is supported by local communities and accounts for coupled relationships between human livelihoods and ecosystem

function (Ali et al, in review). Given the results presented here, I recommend a combination of habitat restoration efforts (grass seeding, manual tree removal, resting range from livestock and elephant conservation) to enhance the recovery of hirola in the long-term.

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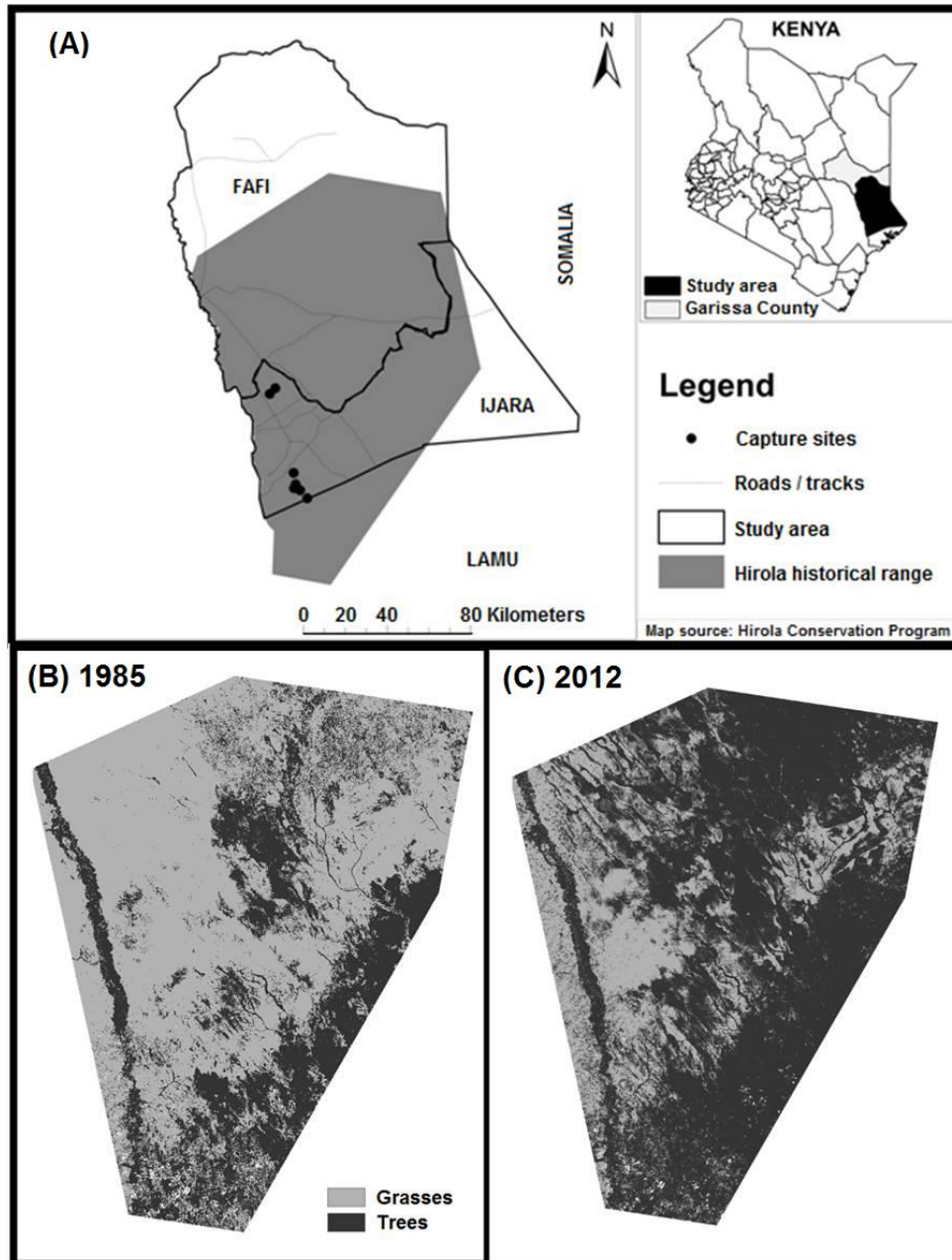
**Tables**

**Table 1:** Summary of hirola home range sizes and the proportions of tree cover within home ranges during both dry and wet season.

<b>Individual ID</b>	<b>Wet Season</b>		<b>Dry Season</b>	
	<b>Home range size (km<sup>2</sup>)</b>	<b>Proportion of tree cover (%)</b>	<b>Home range size (km<sup>2</sup>)</b>	<b>Proportion of tree cover (%)</b>
<b>A</b>	16.6	71.4	14.0	77.3
<b>B</b>	26.1	1.4	27.8	18.1
<b>C</b>	39.3	0.9	31.0	8.8
<b>D</b>	40.0	74.9	40.4	65.9
<b>E</b>	65.0	68.4	38.8	68.1
<b>F</b>	43.3	72.7	133.5	74.2
<b>G</b>	51.0	94.4	235.6	93.7
<b>Mean</b>	40.2 ± 6.0 SE	54.9 ± 14.0SE	74.4 ± 30.7SE	58.0 ± 12.0SE

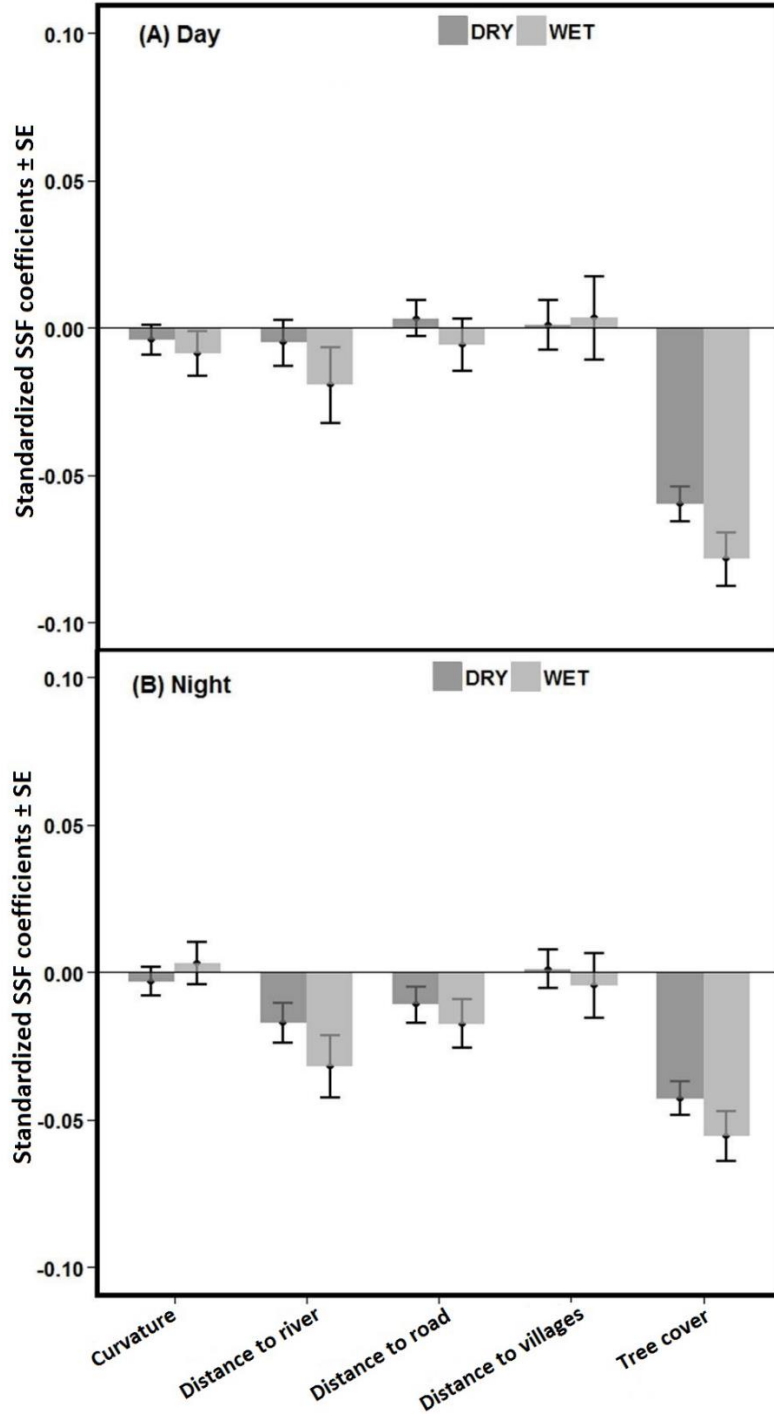
## Figures

**Figure 1:** (A) Study site in Garissa County, Kenya and the historical geographic range of hirola estimated from a minimum convex polygon based on the distribution of hirola in 1963. (B) Tree cover across the hirola's historical range (1985). (C) Tree cover across the hirola's current range (2012). Dark gray represents tree cover and light gray represents grasslands. The linear feature at the west of both images is the Tana River. Tree cover increased 251% between 1985 and 2012.

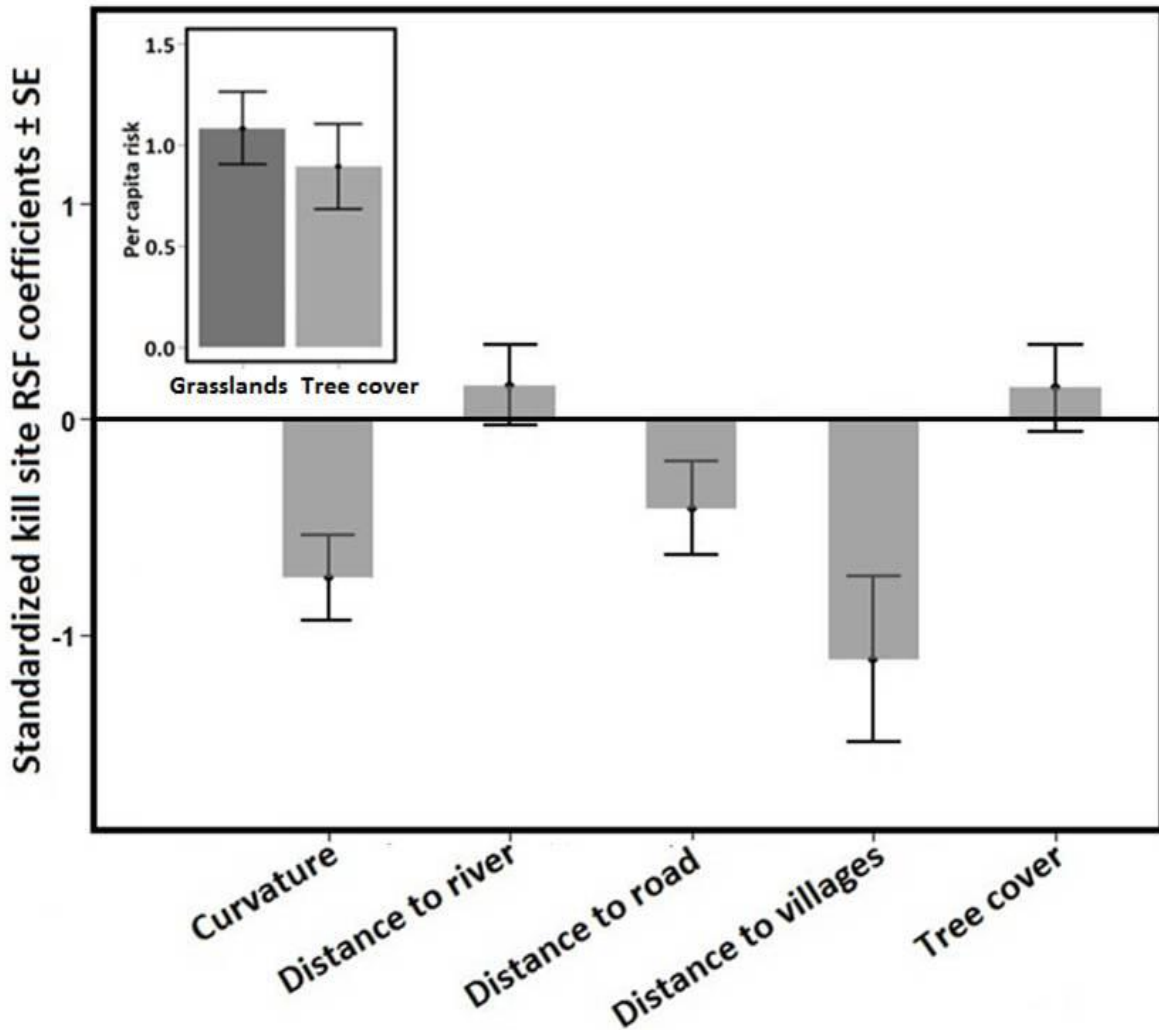




**Figure 2:** Step selection function (SSF) coefficients for the strength of avoidance of landscape variables in (A) day and (B) night by hirola during dry and wet seasons. Note that "river", "road", and "villages" are distance variables, such that a negative coefficient indicates selection for the corresponding variable.



**Figure 3:** Resource selection function (RSF) coefficients for hirola kill sites showing risk of mortality from predation as a function of landscape variables. A positive RSF coefficient indicates a higher than expected chance that a kill site will occur at a location compared to a random location. Note that "river", "road", and "villages" are distance variables, such that a negative RSF coefficient indicates selection for the corresponding variable. Inset is per capita risk of hirola mortality in open and tree cover habitats.



## Chapter 3

### **Evaluating support for rangeland-restoration practices by rural Somalis: an unlikely win-win for local livelihoods and hirola antelope?**

#### **3.1 Introduction**

In semi-arid rangelands, overgrazing, fire suppression, and climate change degrade forage bases, thereby threatening both wildlife populations and pastoral livelihoods (Wilcox & Murphy 1985; Turner & Corlett 1996; Schrott, With & King 2005; Angassa & Oba 2008; Hanke *et al.* 2014). This is especially so in East African rangelands that historically housed a staggering diversity of wildlife alongside pastoralists (Angassa & Oba 2008; Bhola *et al.* 2012). Here, human-wildlife coexistence has relied on benefits of wildlife to livestock and vice versa (Georgiadis *et al.* 2007; Augustine *et al.* 2011; Odadi *et al.* 2011). However, this coexistence is precarious, and can be threatened by increasing livestock densities that cause wildlife populations to decline (Western, Russell & Cuthill 2009; Ogutu *et al.* 2011).

In developing countries, national governments often lack the resources to enforce protection of national parks and reserves (hereafter “protected areas”). In East Africa, nonprotected areas comprise more than 75% of the land surface (Chape *et al.* 2005; Newmark 2008). Here, community-based conservation (hereafter “CBC”)—local involvement aimed at promoting conservation while maintaining or improving people’s standards of living (Berkes 2004)—offers a potential solution, and sometimes the *only* potential solution (Western, Waithaka & Kamanga 2015) to maintaining wildlife populations. However, CBC often is faced with two major challenges. First, CBC may conflate two distinct goals: improvements to pastoral livelihoods and wildlife conservation. Although these objectives are sometimes compatible, the intertwined nature of humanitarian and conservation goals can dilute and

therefore detract from both efforts (Berkes 2004; Chan *et al.* 2007; Waylen *et al.* 2010). Second, an unwillingness of government agencies and NGOs to fully transfer authority to locals (i.e., devolution) can result in inefficiency and a distrust of formal conservation groups by locals (Berkes 2004; Waylen *et al.* 2010).

Restoring habitat for wildlife also has the potential to improve forage for livestock, thereby creating a means through which communities can both actively engage in and benefit from conservation. In turn, local opinions and perceptions can benefit conservation tremendously (Infield 1988; Holmes 2007; Larijani & Yeshodhara 2008; Campbell, Sayer & Walker 2010), such that conservation efforts often are most effective when led by locals (e.g., Lepp & Holland 2006; Sebele 2010; Ingram, Redford & Watson 2012). Despite the apparent recognition of the importance of local involvement, authorities often fail to take into account the diversity of and motivation of community interests (Pimbert & Pretty 1997; Kiss 2004), thereby generating hostility between local communities and the government agencies responsible for wildlife conservation and management (Holmern, Nyahongo & Røskoft 2007; Hazzah, Borgerhoff-Mulder & Frank 2009; Redpath *et al.* 2013). With these challenges in mind, I sought to quantify community attitudes toward rangeland-restoration practices for livestock and hirola (*Beatragus hunteri*). The hirola is regarded the world's most endangered antelope (IUCN 2008), restricted to 1200 km<sup>2</sup> on the Kenya-Somali border. Although they have never been common, hirola have dwindled from ca. 13,000 individuals in 1970 to <500 individuals currently (Probert *et al.* 2015). The remaining population of hirola occurs on pastoral community land that lacks formal protection and Arawale National Reserve, which is the only official protected area lacks attention from conservationists. Hirola historical range occurred in arid grassland which were, which were inhabited by nomadic people and wildlife.

However, colonial policies lead to a shift from nomadism to sedentary pastoralism by encouraging settlements around boreholes and other fixed infrastructure (Niamir-Fuller & Turner 1999; Boone 2005).

Since the mid-1980s, tree cover throughout the hirola's geographic range has increased >250% (Ali et al. in review). Such landscape change has made it more profitable for locals to shift from (grass-eating) cattle (*Bos indicus*) production to (tree/shrub-eating) goat (*Capra hircus*) and camel (*Camelus dromedarius*) production. Elsewhere in sub-Saharan Africa, tree encroachment has been linked directly to a release from browsing caused by megafaunal declines, particularly elephants (Riginos 2009; Goheen *et al.* 2013; Daskin *et al.* 2016). Indeed, in a recent study on hirola movement and habitat selection, tree encroachment was the ultimate driver of hirola habitat availability, more so than access to water or proximity to people (Ali et al. in review). Critically, this study also demonstrated that habitat availability for hirola has declined by 75% between 1984 and 2012 (Ali et al. in review).

In 2012, and in an attempt to curtail further hirola declines, the Ishaqbini Community Conservancy, the Northern Rangelands Trust and Kenya Wildlife Service established a 25 km<sup>2</sup> livestock-free and predator-proof sanctuary to breed hirola and then reintroduce them to wide swathes of their historic range in eastern Kenya. To the extent that tree encroachment was (and continues to be) responsible for low numbers of hirola, the success of this reintroduction effort likely hinges on rangeland restoration and thus the support, perspectives, knowledge, and participation of local communities.

The goals of my research were to: (1) identify socially-acceptable, potential solutions for rangeland restoration; and (2) assess predictors of social acceptance for these rangeland restoration practices by local communities. I identified the following practices as potential

solutions for rangeland restoration, all of which have been demonstrated to enhance grass growth, reduce tree cover, or both in sub-Saharan savannas: manual removal of trees (Riginos 2015); core-area resting of range—restricting grazing from ‘core’ areas to the dry season; (O’Connor *et al.* 2010); livestock reduction (Odadi *et al.* 2011); controlled or ‘prescribed’ burns (Sensenig, Demment & Laca 2010); soil ripping (Kinyua *et al.* 2010); seeding and fertilization (Kinyua *et al.* 2010); and elephant conservation (Duffy *et al.* 2002; Goheen and Palmer 2010). I show that pastoralist communities in eastern Kenya are supportive of several of these rangeland-restoration practices, which could improve the quality of hirola habitat alongside local livelihoods.

## **3.2 Methods**

### **3.2.1 Study area**

I conducted my study in Ijara (latitude 1°36’S, longitude 40°32’E) and Fafi (latitude: -0°25’ S, longitude: 40°13’E) subcounties of Garissa County in eastern Kenya. These areas represent one of the most underdeveloped and economically marginalized areas in East Africa. Communities rely on livestock production, and pastoralism has been practiced in the region for hundreds of years. Livestock herds are composed of goats, cattle, camels, and donkeys (*Equus asinus*). Here, pastoralists comprise two Somali sub-tribes: the Abudwaq in Fafi and the Abdalla in Ijara, collectively referred to as the Talamoge Ogadens.

My study area lies between 40 m and 250 m above sea level and is underlain by well-drained sandy soils. Rainfall in my study area is bimodal, with the long rainy season (locally referred to as *Guu*) occurring in April to June and the short rainy season (locally referred to as *Deir*) occurring from November to December. Two punctuated dry periods occur between the

wet seasons: the short dry season in January-March (locally referred to as *Jilal*) and the long dry season which occurs from July-October (locally referred to as *Hagaa*). The mean annual rainfall varies between 350 mm in Fafi to 550 mm in Ijara (Bunderson 1979, 1981). The preferred habitat of hirola occurs on open grassland in the 400-550 mm rainfall zone in both sub-counties (Bunderson 1981, Ali et al. in review). Average annual temperatures in the region range from 21°C to 30°C (Muchena 1987). The most common ungulates in the area include the reticulated giraffe (*Giraffa camelopardalis reticulata*), gerenuk (*Litocranius walleri*), lesser kudu (*Tragelaphus imberbis*), waterbuck (*Kobus ellipsyprimnus*), and Kirk's dik-dik (*Madoqua kirkii*). Large carnivores in the region include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), and African wild dogs (*Lycaon pictus*).

### **3.2.2 Survey design**

From 2013-2014, I conducted surveys using a semi-structured questionnaire (Liu *et al.* 2011; Okello *et al.* 2011; Table 1). Prior to administering the surveys, questionnaires were subjected to expert review with the Kenya Wildlife Service and pilot tested with local communities (n = 80 pilot-tested respondents, 16 respondents in each of five villages). Across the two subcounties, I sampled a total of 10 villages: Gababa, Hara, Korisa, Masalani, and Qotile in Ijara, and Aliimitch, Bura, Galmagala, Garasweno and Mansabubu in Fafi (Fig. 1). Each of the 10 villages was randomly selected, subject to the constraint that sampled communities were not adjacent to one another (mean distance between sampled villages = 28.0 km  $\pm$  9.0 SE). I randomly sampled 131 respondents from these 10 villages (range = 6-32 respondents per village, mean 14.7  $\pm$  3.0 SE respondents per village). Each respondent belonged to a unique household, and I surveyed only a single respondent per household. I defined households as

members of the same family where a single individual (mother or father) is considered the head of the family unit (Kideghesho, Røskaft & Kaltenborn 2007). To encourage participation in my surveys, respondents were not asked to indicate their names. I trained one local per village to administer the questionnaires in each of the villages. I recorded the following socialdemographic (predictor) variables associated with each respondent: gender, age, level of education (no formal education, primary, and high school), years of residency in the village, and livestock wealth (the total number of livestock owned by the household).

Before administering questionnaires, I operationally defined the seven rangelandrestoration practices to individuals as follows:

- *Manual removal of trees*: the physical cutting, uprooting or breaking of branches in attempt to restore grassland at scales of hundreds of hectares.
- *Core-area resting of rangeland*: the cessation of livestock grazing across hundreds of hectares (i.e., ‘core’ areas) during the wet season to allow the regrowth of grasses, that then can be grazed by livestock during the dry season.
- *Livestock reduction*: the voluntary sale or butchering of 20% of individual livestock in a respondent’s herd. These 20% could be any combination of goats, sheep, and cattle.
- *Controlled burns*: the prescribed burning of tree-encroached areas at scales of hundreds of hectares.
- *Soil ripping*: a type of tillage in which compacted soil is broken open manually (but not removed) at scales of hundreds of hectares.
- *Seeding and fertilization*: the planting of native grass seeds alongside fertilizer (manure) at scales of hundreds of hectares.



- *Elephant conservation*: community-based protection and conservation of elephants through anti-poaching and improved communication among locals and authorities to increase tolerance towards elephant herds to reside on community rangelands.

### **3.2.3 Data analysis**

To analyze responses from questionnaires, I used a classification and regression tree (CART) approach, using the *rpart* package in R version 3.03 (Therneau & Atkinson 2010). I used CARTs to examine social-demographic predictors of acceptance for each of the proposed rangeland-restoration practices. CARTs can be used for the analysis of numeric and nonnumeric response data with missing values, as well as non-linear datasets (De'ath & Fabricius 2000). CARTs also allow for complex interactions among covariates with fewer specifications, thus making it possible to identify predictors underlying social acceptance of rangelandrestoration practices (Sutton 2005). Further, and unlike multiple regression, CARTs accounts for multicollinearity through best-split criteria and bias minimization in selection of predictor variables (Kim & Loh 2011)

To help with interpretation of CART output, I employed a splitting rule function using the *rattle* package in R version 3.03 (Williams 2009; R Development Core Team 2014), which utilizes a squared residual minimization algorithm (Timofeev 2004). The algorithm computes and minimizes the sum of variances for corresponding left and right nodes and ends when the observations (the number) in each of the two nodes does not exceed a predefined required minimum. To validate each CART, I used the relative error, calculated by  $1 - R^2$ , and obtained the complexity parameter (*cp*) for each of the seven CART models (i.e., one for each rangelandrestoration practice). The cross-validation procedure penalizes (prunes off) any split

in the model that does not improve the fit by  $cp$ , which results in selection of “optimal” regression trees.

CART models do not provide predictions with probabilistic levels or confidence intervals (Yohannes & Webb 1999), which is of interest in my study. To complement my efforts with CART, I developed a conditional inference tree (CIT) approach using the *party* package in R version 3.03 (Hothorn, Hornik & Zeileis 2006; R Development Core Team 2014). Conditional inference trees reduce biases in predictor selection, thus enabling selection of predictors with the most possible splits or missing values (Strobl *et al.* 2008). In addition, conditional inference trees make it possible to compute levels of significance and provide  $p$ values (Hothorn, Hornik & Zeileis 2006).

Finally, I used generalized linear models (GLMs) to model predictors of answers to survey questions. GLMs are less prone to overfitting and generate easily interpreted regression coefficients, which can be problematic for CARTs and CITs. These questions addressed how social-demographic predictors influenced answers with a discrete value (“Strongly Agree”, “Agree”, “Neutral/Undecided”, “Disagree”, “Strongly Disagree”). I combined “Strongly Agree” and “Agree” into a single category (“Agree”), and “Strongly Disagree” and “Disagree” into a single category (“Disagree”). To examine relationships between acceptance of rangelandrestoration practices and social-demographic predictors in my CART, CIT, and GLM models, I visually inspected plots from the model outputs in addition to assessing measures of goodnessof-fit (through coefficients, residuals, variance and deviance (Arentze & Timmermans 2004)). I also identified the most important social-demographic predictors of acceptance for each rangeland-restoration practice using mean square errors and  $p$ -values.

### 3.3 Results

In order of agreement, participants were most supportive of elephant conservation, manual removal of trees, grass seeding and fertilization, and core-area resting (Table 2, Table S1). In contrast, participants were less supportive of voluntary reduction of livestock, soil ripping, and controlled burns (Table 2, Table S1). I present the CARTs illustrating social-demographic predictors for attitudes toward elephant conservation (Fig. 2A) and livestock reduction (Fig. 2B) that represent the rangeland-restoration practices toward which respondents were most and least supportive, respectively. Livestock wealth was the primary predictor of respondents' attitudes toward elephant conservation: support for elephant conservation was strongest for households owning <150 head of livestock. Age was the most important predictor of locals' attitudes toward livestock reduction, as respondents  $\geq 50$  years old were more supportive of voluntary reductions in livestock. A summary of the CART output is presented in Table 2, and the remaining five CARTs are appended in the supplementary material (Figs. S1-S5). The remaining two CITs associated with statistically significant  $p$ -values (for core-area resting, and for seeding and fertilization) are appended in the supplementary material (Figs. S3 and S4).

Livestock wealth was (1) the most important social-demographic predictor of attitudes toward 5 of the 7 rangeland-restoration practices (soil ripping, controlled burns, manual removal of trees, grass seeding and fertilization, and elephant conservation; Table 2); and (2) significantly and negatively related to support for soil ripping, grass seeding and fertilization, and elephant conservation (Table 3). Level of formal education was the most important social demographic predictor explaining attitudes toward core-area resting: respondents lacking formal education did not support core-area resting (Table 2, Table 3). Age was the most important social-demographic predictor for attitudes toward livestock reduction, as younger

respondents were less supportive of reducing their herd sizes (Table 2, Table 3). Gender of the household head was not a statistically significant predictor for acceptance toward any of the rangeland-restoration practices.

Results from CITs were congruent with those of CARTs (Fig. 2), with livestock wealth ( $P = 0.004$ ) and years of residency ( $P = 0.002$ ) as the primary determinants for acceptance of elephant conservation, and age the most important determinant for acceptance of livestock reduction ( $P = 0.039$ ).

### **3.4 Discussion**

I explored attitudes of pastoralists toward seven rangeland-restoration practices, all of which have been demonstrated previously to enhance range quality. Over 75% of the hirola's range has experienced tree encroachment, likely caused by some combination of elephant extirpation, overgrazing by livestock, and fire suppression (Ali et al. in review). Small population sizes of hirola have coincided with tree encroachment, and the few hirola that persist in eastern Kenya strongly avoid woody cover (Ali et al. in review). In addition to its detrimental impact on hirola, this widespread conversion of grassland to shrubland has negatively impacted the livelihoods of pastoralists in Eastern Kenya (Ali, personal observation). Consequently, the majority of pastoralists in my study area are supportive of rangeland-restoration in general, and elephant conservation, grass seeding and fertilization, manual removal of trees, and core-area resting in particular.

My findings are aligned with those of a recent study in southern Kenya in which the majority of pastoralists supported the conservation of elephants in community rangelands (Browne-Nuñez, Jacobson & Vaske 2013). While I acknowledge that the high level of

enforcement associated with elephant conservation outside of formally-protected areas would be immense, I believe that any future attempts to restore rangeland would be well-served to also protect newly-recolonizing elephant herds *in situ* within Ijara and Fafi subcounties. After an absence of nearly three decades (Ali et al. in review), elephants recently have begun to recolonize Ijara and Fafi sub-counties naturally, although they persist only in low numbers and typically pass through this region as they move between Boni National Reserve to the east and Tsavo National Park to the southwest. Integration of community activities and elephant conservation has been successful elsewhere in Kenya (e.g., Kuriyan 2002), and I recommend that government agencies and non-government organizations afford every protection possible to bolster plummeting elephant numbers and as a potential means to restore habitat for hirola. In Ijara and Fafi, communities expressed strong support for elephant conservation because of (1) a perceived link between the presence of elephants and profitable levels of cattle production in the 1960s and 1970s (which likely are a cause and an effect, respectively, of open-grassland habitat); and (2) ecosystem services provided by elephants (e.g., seed dispersal, excavation and maintenance of watering holes). Interestingly, none of the individuals I surveyed invoked economic gains from tourism as a rationale for conserving elephants.

I am encouraged that a large fraction of pastoralists were supportive of grass seeding and fertilization for rangeland restoration. The acceptance of seeding and fertilization conforms with its demonstrated potential as a tool in both wildlife conservation and poverty reduction (Kinyua *et al.* 2010; Mganga *et al.* 2015). Additionally, manual removal of trees was strongly supported by locals and may be another option to facilitate rangeland restoration. The long term persistence of hirola on communal lands may very well hinge on active habitat management such as manual removal of trees, which may provide local employment and provisioning of

charcoal for households (Mwampamba *et al.* 2013). Finally, by exploiting the same areas at different points in time, core-area resting holds potential as a means through which hirola, other grazing wildlife, and livestock may coexist (see also Augustine *et al.* 2011, Odadi *et al.* 2011).

In many regions of Africa, overgrazing (by livestock) has triggered rangeland degradation where pastoralism is the dominant land-use (e.g. Dodd 1994; Wessels *et al.* 2007; Hanke *et al.* 2014). Perhaps not surprisingly, participants in my surveys were least supportive of voluntary reductions in livestock among potential rangeland-restoration practices. Although livestock wealth is a measure of individual status in Somali society, years of residency was the only social-demographic predictor strongly associated with support for livestock reduction. This suggests that long-term residents are less concerned with their own social status, or have borne witness to links between rangeland degradation and increasing numbers of livestock in the region.

A major challenge for the future is ensuring that livestock owners do not simply increase livestock numbers in light of improved range, leading to a classic Tragedy of the Commons (Hardin 1968). Since livestock consume forage that otherwise could be utilized by hirola, hirola conservation hinges ultimately on a level of local restraint: some critical fraction of restored rangeland must be made available as food and habitat for hirola (Swallow & Bromley 1995; Hackel 1999). Such long-term, sustainable yields for livestock, hirola, and other wildlife necessitate (1) well-defined, widely-recognized boundaries around rangelands associated with communities within the hirola's range, with exclusion of outside parties; (2) rules for the provision of grazing lands to individuals within communities, coupled with sanctions for those who violate such rules; and (3) participatory decision-making, in which individuals are encouraged to determine #1 and #2 independently of higher-level authorities

(Ostrom 1990). Ultimately, implementation of these principles requires strong, prominent leadership through community elders coupled who, in turn, have strong public support (Kothari, Camill & Brown 2013; Hazzah *et al.* 2014; see also Gutierrez, Hilborn & Defeo 2011).

Human-wildlife conflict often constrains opportunities for habitat restoration, species reintroductions, and other endeavors central to wildlife conservation. I have demonstrated that pastoralists in eastern Kenya are supportive of several rangeland-restoration practices, which could improve hirola habitat alongside local livelihoods. Implementation of these practices and, ultimately, the persistence of hirola depends on the willingness of communities to enact these measures.

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## Tables

**Table 1:** Questions posed to Somali pastoralists in semi-structured questionnaires

<b>Which of the following restoration practices will you accept for range improvement for hirola and livestock?</b>	<b>Response</b>
<b>Manual removal of trees</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree
<b>Core area resting</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree
<b>Livestock reduction</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree
<b>Controlled burns</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree
<b>Soil ripping (i.e., soil disking)</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree
<b>Seeding and fertilization</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree

**Table 1(Continued):** Questions posed to Somali pastoralists in semi-structured questionnaires

<b>Which of the following restoration practices will you accept for range improvement for hirola and livestock?</b>	<b>Response</b>
<b>Elephant conservation</b>	1. Strongly disagree 2. Disagree 3. Neutral or undecided 4. Agree 5. Strongly agree

**Table 2:** Summary of CART output. Rangeland-restoration practices are in ascending order of agreement from respondents (i.e., livestock reduction was the least-supported practice while elephant conservation was the most-supported practice)

<b>Range-restoration Practice</b>	<b>Social-demographic importance (most to least agreement)</b>	<b>Variance explained at first split</b>	<b>Total % variance explained</b>
<b>Livestock reduction</b>	<ul style="list-style-type: none"> <li>• Age</li> <li>• Livestock wealth</li> <li>• Length of residency</li> <li>• Gender</li> <li>• Education</li> </ul>	30.5	94.1
<b>Soil ripping</b>	<ul style="list-style-type: none"> <li>• Livestock wealth</li> <li>• Length of residency</li> <li>• Age</li> <li>• Gender</li> <li>• Education</li> </ul>	21.1	88.2
<b>Controlled burns</b>	<ul style="list-style-type: none"> <li>• Livestock wealth</li> <li>• Length of residency</li> <li>• Age</li> <li>• Education</li> <li>• Gender</li> </ul>	23.1	28.0
<b>Core-area resting</b>	<ul style="list-style-type: none"> <li>• Education</li> <li>• Length of residency</li> <li>• Livestock wealth</li> <li>• Age</li> <li>• Gender</li> </ul>	27.8	89.9
<b>Seeding and fertilization</b>	<ul style="list-style-type: none"> <li>• Livestock wealth</li> <li>• Gender</li> <li>• Age</li> <li>• Education</li> <li>• Length of residency</li> </ul>	19.0	51.4
<b>Manual removal of trees</b>	<ul style="list-style-type: none"> <li>• Livestock wealth</li> <li>• Length of residency</li> <li>• Education</li> <li>• Age</li> <li>• Gender</li> </ul>	30.7	80.6

**Table 2 (Continued):** Summary of CART output. Rangeland-restoration practices are in ascending order of agreement from respondents (i.e., livestock reduction was the least-supported practice while elephant conservation was the most-supported practice)

<b>Range-restoration Practice</b>	<b>Social-demographic importance (most to least agreement)</b>	<b>Variance explained at first split</b>	<b>Total % variance explained</b>
<b>Elephant conservation</b>	<ul style="list-style-type: none"> <li>• Livestock wealth</li> <li>• Length of residency</li> <li>• Education</li> <li>• Age</li> <li>• Gender</li> </ul>	26.4	72.5

**Table 3:** Regression coefficients of social-demographic predictors for rangeland-restoration practices as obtained from GLMs. *P*-values < 0.10 are reported; *p*-values <0.05 are underlined. Corresponding estimates of the slope of the GLM fit are given in parentheses.

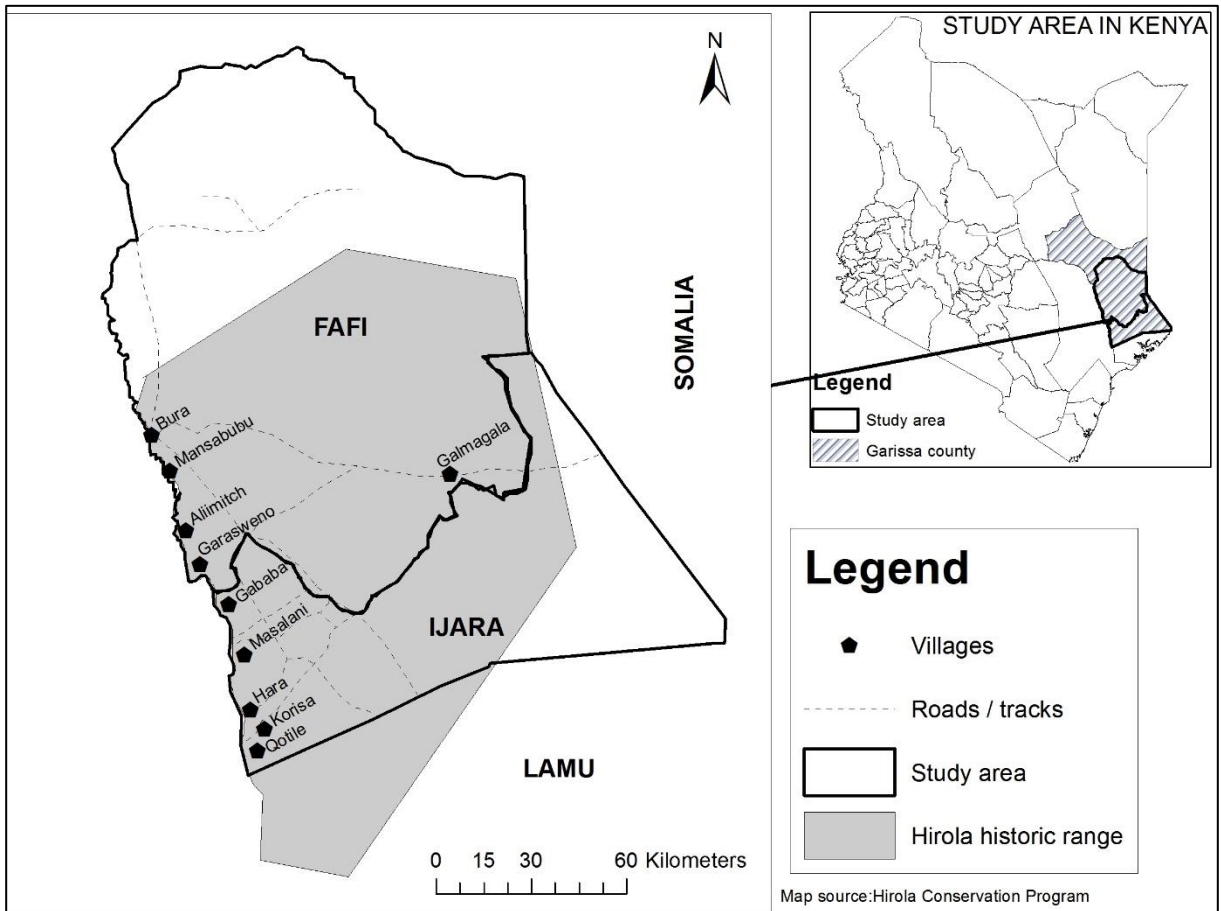
			<b>Livestock reduction</b>	<b>Soil ripping</b>	<b>Controlled burning</b>	<b>Core-area resting</b>	<b>Manual removal of trees</b>	<b>Seeding and fertilization</b>	<b>Elephant conservation</b>
<b>Age</b>	Agree		0.07 (0.01)	-	-	-	-	-	-
	Disagree		<u>0.02</u> (-0.01)	-	-	-	-	-	-
<b>Gender</b>	Agree	M	-	-	-	-	-	-	-
		F	-	-	-	-	-	-	-
	Disagree	M	-	-	-	-	-	-	-
		F	-	-	-	-	-	-	-
<b>Level of education</b>	Agree	P	-	-	-	-	-	-	-
		H	-	-	-	-	-	-	-
		N	-	-	-	<u>0.02</u> (-0.48)	-	-	-
	Disagree	P	-	-	-	-	-	-	-
		H	-	-	-	-	-	-	-
		N	-	-	-	0.08 (0.34)	-	-	-
<b>Livestock wealth</b>	Agree		-	<u>0.05</u> (-0.001)	-	-	-	<u>0.0004</u> (-0.001)	<u>0.002</u> (-0.001)
	Disagree		-	-	-	-	-	<u>0.0006</u> (0.001)	<u>0.0001</u> (0.001)
<b>Years of residency</b>	Agree		<u>0.05</u> (-0.005)	-	-	0.07 (-0.01)	-	-	<u>0.003</u> (0.005)
	Disagree		0.07 (0.005)	-	-	-	-	-	<u>0.03</u> (-0.004)

Note: M=Male, F=Female, P = Primary school, H = High school, N = No formal education

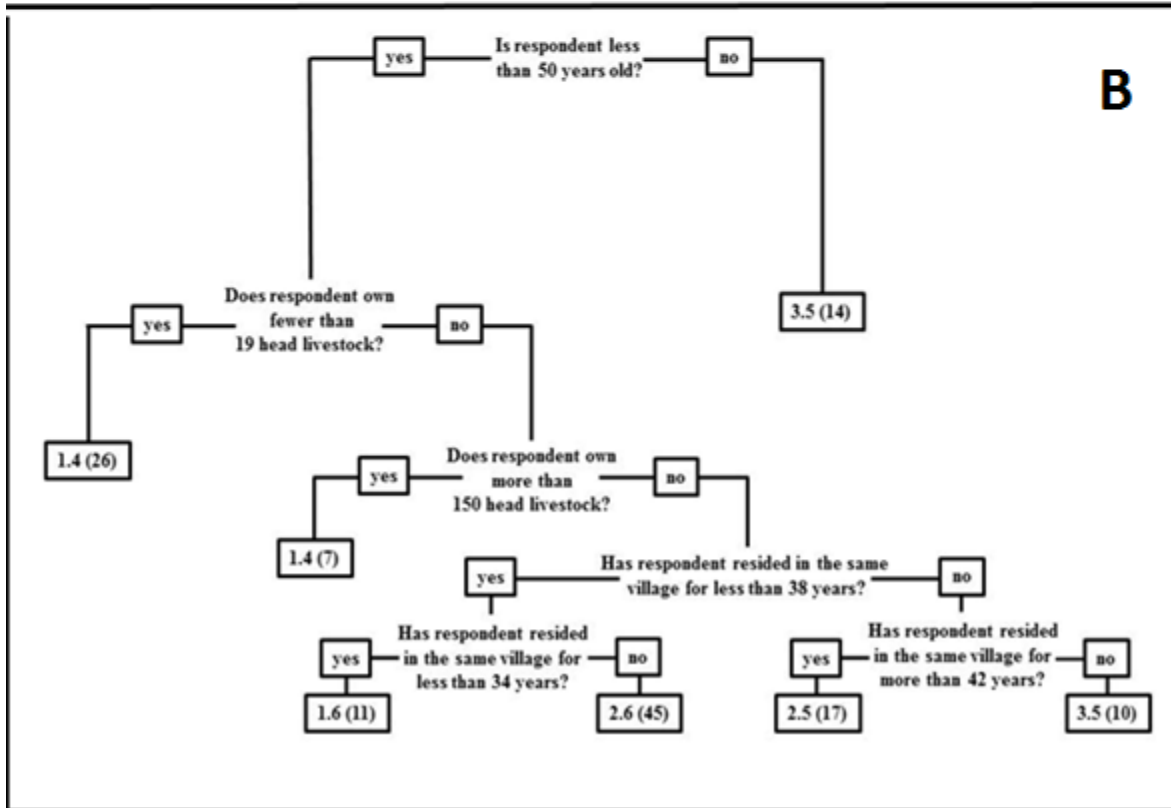
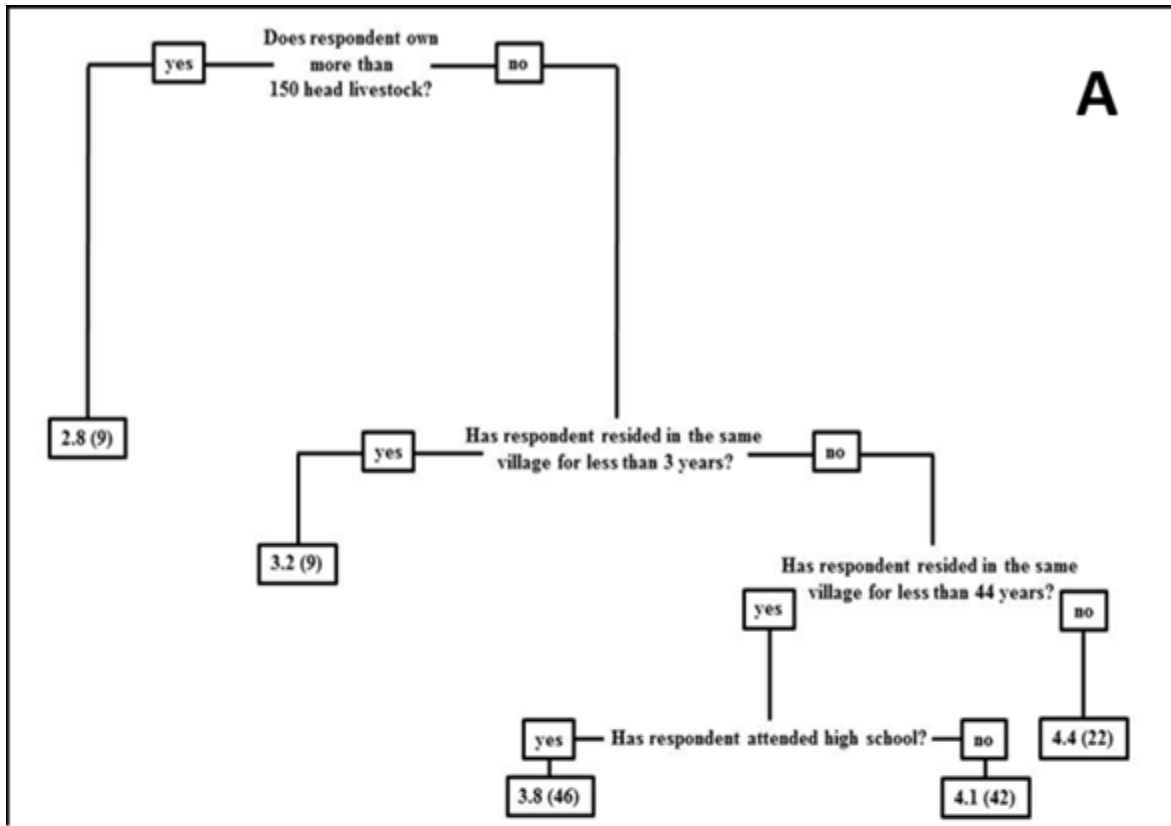


## Figures

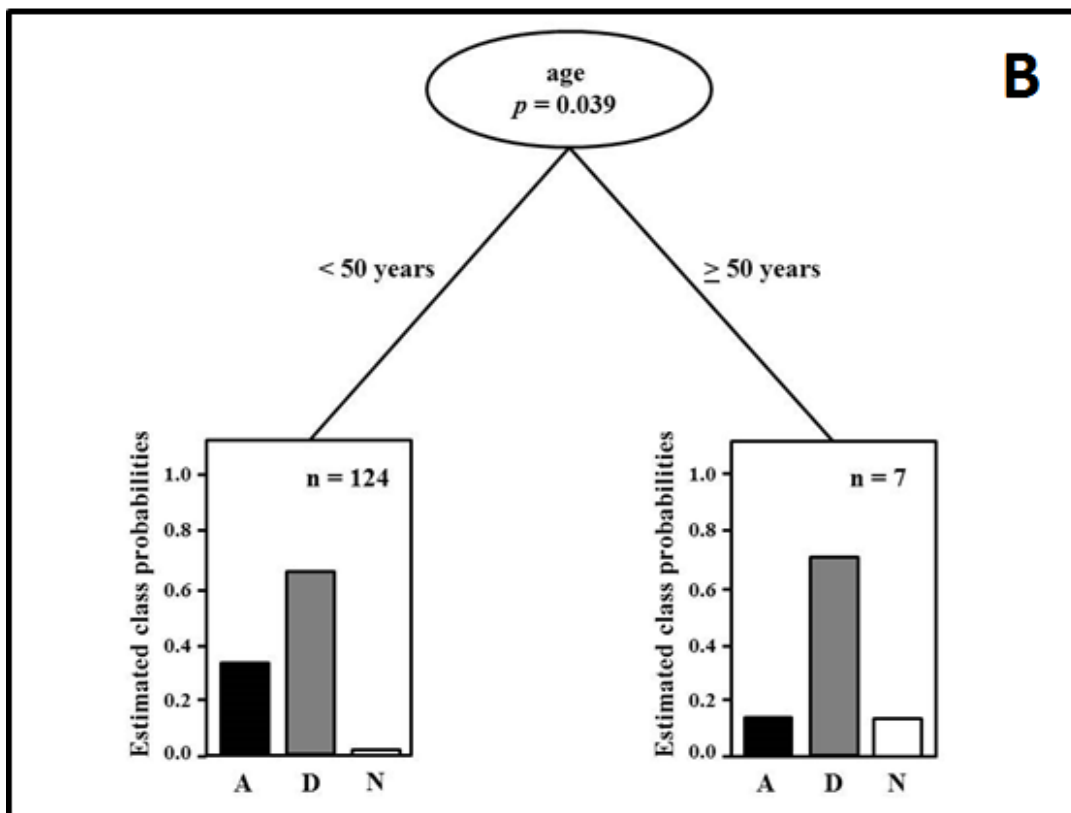
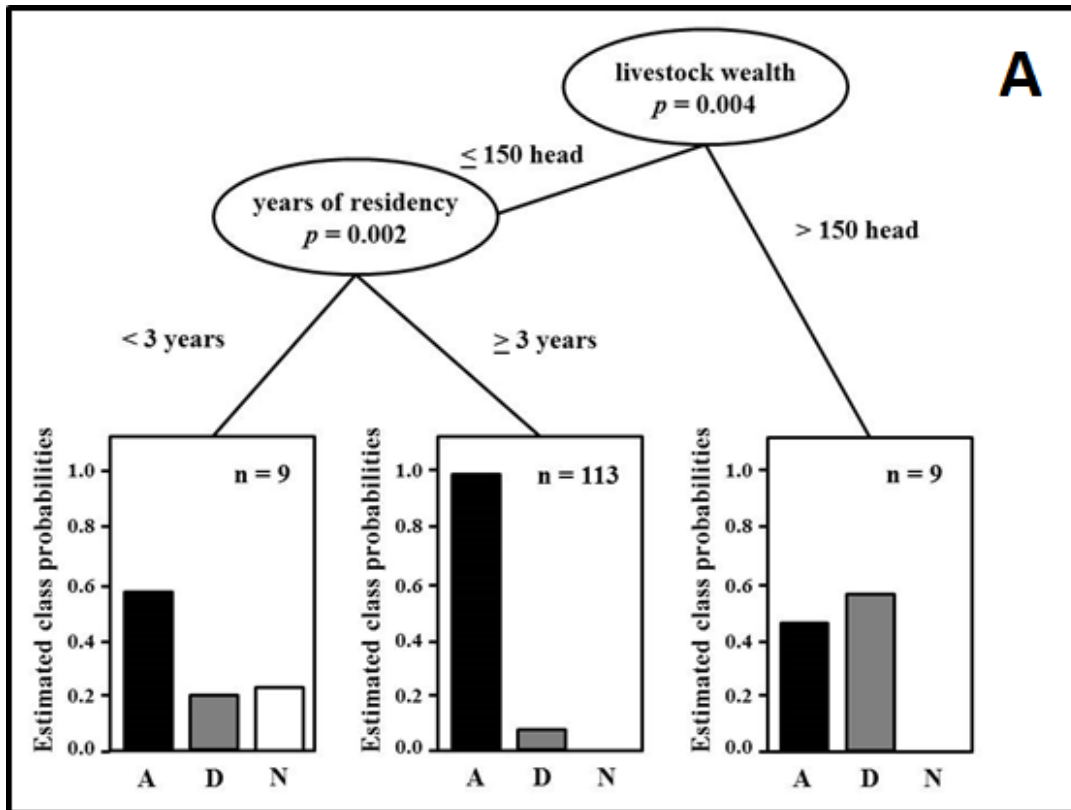
**Figure 1:** Communities in Ijara and Fafi sub-counties in Garissa County, Kenya and the historic geographic range of hirola (estimated from a minimum convex polygon based on a 1963 hirola distribution).



**Figure 2:** Optimal CART models for responses to the questions A) “Do you support elephant conservation as a strategy to improve range quality?”; and B) “Do you support reducing the number of livestock you own to improve range quality?” Predictor variables are defined at each corresponding branch split. Terminal nodes represent the mean response (ranging from 1-5, where 1 represents the strongest level of disagreement, and 5 represents the strongest level of agreement); for each terminal node, numbers of respondents are included in parentheses. Branch lengths are proportional to the amount of variance explained by the predictor variable at the split. For example, the group most supportive of elephant conservation are individuals owning less than 150 head of livestock who have resided in the same village for more than 44 years (22 individuals with a mean acceptance score of 4.4), while the group least supportive of elephant conservation (mean acceptance score of 2.8) are the nine individuals who own more than 150 head of livestock.



**Figure 3:** Conditional inference trees depicting the estimated proportions and statistical significance of social-demographic predictors for the questions A) “Do you support elephant conservation as a strategy to improve range quality?”; and B) “Do you support reducing the number of livestock you own to improve range quality?” The prefixes A stand for Agree (those responding “Strongly agree” or “Agree” to the question), D for Disagree (those responding “Strongly disagree” or “Disagree”), and N for Neutral (those responding “Neutral” or “Undecided”).



## Supplementary Materials

### Chapter 1 (Tables)

**Table S1:** Sighting of large carnivores within the Ishaqbini Community Conservancy and Ijara rangelands (sightings day<sup>-1</sup> km<sup>-2</sup>)

<b>Predator species</b>	<b>Conservancy</b>	<b>Outlying areas</b>
<b>Cheetah</b>	0.10	0.09
<b>Caracal</b>	0.08	0.07
<b>Wild dogs</b>	0.04	0.04
<b>Lions</b>	0.04	0.03
<b>Leopard</b>	0.02	0.01

**Table S2:** Hirola groups identification and repeatability validations across settings based on agreements among team members.

**A: Conservancy**

<b>Group Number</b>	<b>Count1</b>	<b>Count2</b>	<b>Verified count</b>	<b>%agreement between count 1 and verified</b>	<b>%agreement between count 2 and verified</b>	<b>average % agreement between count 1 and 2</b>
<b>1</b>	4	3	4	100.0	75.0	87.5
	5	4	4	125.0	100.0	112.5
	6	5	6	100.0	83.3	91.7
<b>2</b>	5	4	5	100.0	80.0	90.0
	5	6	7	71.4	85.7	78.6
	7	5	7	100.0	71.4	85.7
	7	6	6	116.7	100.0	108.3
	5	4	6	83.3	66.7	75.0
<b>3</b>	5	8	7	71.4	114.3	92.9
	15	17	23	65.2	73.9	69.6
	24	18	24	100.0	75.0	87.5
	19	18	21	90.5	85.7	88.1
<b>4</b>	17	21	21	81.0	100.0	90.5
	10	9	10	100.0	90.0	95.0
	9	10	10	90.0	100.0	95.0
	15	10	10	150.0	100.0	125.0

**A: Conservancy (Table Continued)**

<b>Group Number</b>	<b>Count1</b>	<b>Count2</b>	<b>Verified count</b>	<b>%agreement between count 1 and verified</b>	<b>%agreement between count 2 and verified</b>	<b>average % agreement between count 1 and 2</b>
	10	9	11	90.9	81.8	86.4
	11	8	11	100.0	72.7	86.4
	7	11	11	63.6	100.0	81.8
<b>5</b>	11	9	11	100.0	81.8	90.9
	12	8	12	100.0	66.7	83.3
<b>6</b>	8	10	12	66.7	83.3	75.0
<b>Overall mean % agreement between verified counts</b>						<b>89.8</b>

**Note:** We validated the number of individuals from each count (1 and 2) by dividing with the verified count and multiplying by 100 to obtain the percent agreements



**B: Sanctuary**

<b>Group Number</b>	<b>Count1</b>	<b>Count2</b>	<b>Verified count</b>	<b>%agreement between count 1 and verified</b>	<b>%agreement between count 2 and verified</b>	<b>average % agreement between count 1 and 2</b>
<b>1</b>	14	15	16	87.5	93.8	90.6
	13	15	16	81.3	93.8	87.5
	16	14	16	100.0	87.5	93.8
<b>2</b>	14	12	14	100.0	85.7	92.9
	8	10	14	57.1	71.4	64.3
	10	13	12	83.3	108.3	95.8
<b>3</b>	5	2	4	125.0	50.0	87.5
<b>4</b>	8	6	8	100.0	75.0	87.5
	7	4	8	87.5	50.0	68.8
	5	4	8	62.5	50.0	56.3
<b>5</b>	6	10	8	75.0	125.0	100.0
	6	4	2	300.0	200.0	250.0
	5	6	6	83.3	100.0	91.7
<b>6</b>	7	5	6	116.7	83.3	100.0
<b>Overall mean % agreement between verified counts</b>						
<b>97.6</b>						

**C: Outlying Areas**

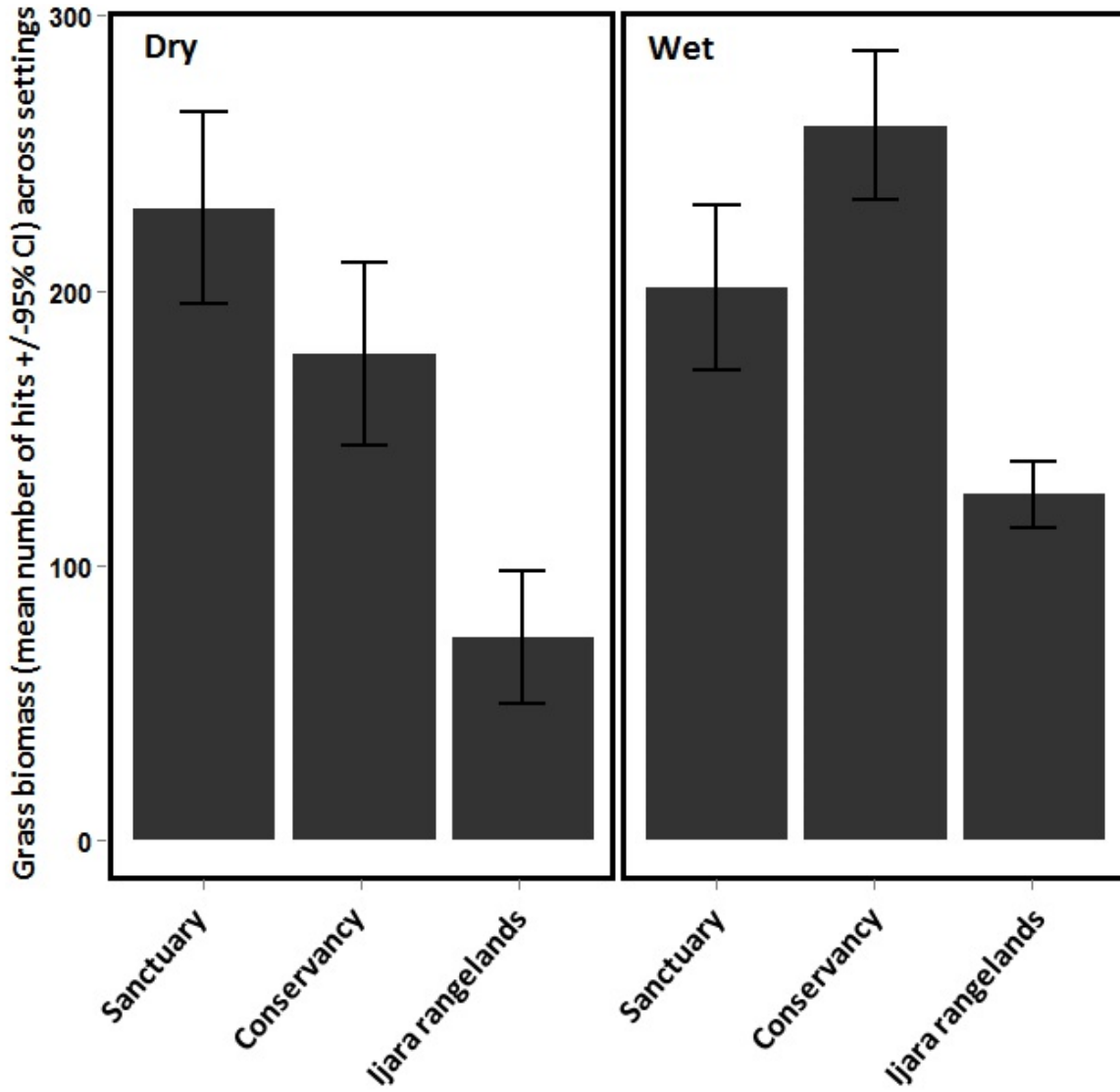
<b>Group Number</b>	<b>Count 1</b>	<b>Count 2</b>	<b>Verified</b>	<b>%agreement between count 1 and verified</b>	<b>% agreement between count 2 and verified</b>	<b>average % agreement between count 1 and 2</b>
<b>1</b>	10	9	11	90.9	81.8	86.4
	7	10	11	63.6	90.9	77.3
	13	9	11	118.2	81.8	100.0
	15	14	11	136.4	127.3	131.8
	9	12	10	90.0	120.0	105.0
	12	9	12	100.0	75.0	87.5
	11	12	12	91.7	100.0	95.8
<b>2</b>	7	8	9	77.8	88.9	83.3
	9	6	9	100.0	66.7	83.3
	4	5	5	80.0	100.0	90.0
	7	6	6	116.7	100.0	60.0
<b>3</b>	5	7	7	71.4	100.0	83.3
	8	6	7	114.3	85.7	108.3
<b>4</b>	4	4	5	80.0	80.0	85.7
	5	4	5	100.0	80.0	100.0
	5	6	6	83.3	100.0	80.0
	5	4	7	71.4	57.1	90.0
<b>5</b>	3	4	5	60.0	80.0	91.7
	4	5	5	80.0	100.0	75.0
	4	5	5	80.0	100.0	92.9
<b>6</b>	2	2	3	66.7	66.7	64.3

**C: Outlying Areas (Table Continued)**

<b>Group Number</b>	<b>Count 1</b>	<b>Count 2</b>	<b>Verified</b>	<b>%agreement between count 1 and verified</b>	<b>% agreement between count 2 and verified</b>	<b>average % agreement between count 1 and 2</b>
	6	4	7	85.7	57.1	70.0
	7	4	7	100.0	57.1	90.0
	7	5	5	140.0	100.0	90.0
<b>7</b>	5	8	9	55.6	88.9	137.5
<b>8</b>	5	4	5	100.0	80.0	78.6
	7	1	7	100.0	14.3	66.7
<b>Overall mean % agreement between verified counts</b>						<b>87.7</b>

Chapter 1 (Figures)

Figure S1: Understory grass biomass (mean number of hits +/- 95% CI).



## Chapter 2 (Tables)

**Table S1:** Landsat scenes used in classified image composites.

<b>Early image date</b>	<b>Current image date</b>
Landsat 5 – 2/21/1985	Landsat 7 – 01/23/2012
Landsat 5 – 4/10/1985	Landsat 7 – 02/05/2011
Landsat 5 – 3/9/1985	Landsat 7 – 02/23/2012
Landsat 5 – 1/23/1986	Landsat 7 – 05/30/2012

**Table S2:** Model rankings according to AIC for hirola step selection functions (wet season)

<b>Time</b>	<b>Model variables</b>	<b>K</b>	<b>LL</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b><math>\omega_i</math></b>
Day	Tree cover	4	-69702.0	139412.0	0.00	0.16
	River + Tree cover	5	-69701.3	139412.5	0.49	0.13
	Curvature + Tree cover	5	-69701.3	139412.7	0.64	0.12
	Curvature + River + Tree cover	6	-69700.6	139413.2	1.13	0.09
	River + Road + Tree cover	6	-69700.9	139413.8	1.73	0.07
	Village + Tree cover	5	-69701.9	139413.8	1.79	0.07
	Road + Tree cover	5	-69702.0	139413.9	1.88	0.06
	Curvature + River + Road + Tree cover	7	-69700.2	139414.4	2.38	0.05
	Curvature + Village + Tree cover	6	-69701.2	139414.5	2.44	0.05
	Road +Village + Tree cover	6	-69701.3	139414.5	2.47	0.05
	Curvature + Road + Tree cover	6	-69701.3	139414.6	2.52	0.05
	Curvature + River + Village + Tree cover	7	-69700.6	139415.1	3.11	0.03
	Road + Village + Tree cover	6	-69701.7	139415.5	3.44	0.03
	River + Road + Village + Tree cover	7	-69700.9	139415.8	3.72	0.02
Night	River + Road + Tree cover	6	-70456.8	140925.5	0.00	0.36
	Curvature + River + Road + Tree cover	7	-70456.7	140927.3	1.82	0.14
	River + Road + Village + Tree cover	7	-70456.7	140927.4	1.91	0.14
	River + Tree cover	5	-70459.0	140927.9	2.39	0.11

**Table S2 (Continued):** Model rankings according to AIC for hirola step selection functions (wet season)

<b>Time</b>	<b>Model variables</b>	<b>K</b>	<b>LL</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b><math>\omega_i</math></b>
	Curvature + River + Road + Village + Tree cover	8	-70456.6	140929.2	3.73	0.06
	River + Village + Tree cover	6	-70458.6	140929.3	3.74	0.06

The models were fitted using a generalized linear mixed model and evaluated using maximum likelihood method for each variable where K is number of degrees of freedom, LL the log-likelihood, AIC the Akaike Information Criterion,  $\Delta$ AIC is the difference in AIC values and  $\omega_i$  is the weight. Only models with  $\Delta$ AIC  $\leq$  4.0 presented.

**Table S3:** Model rankings according to AIC for hirola step selection functions (dry season).

<b>Time</b>	<b>Model variables</b>	<b>K</b>	<b>LL</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b><math>\omega_i</math></b>	
Day	Tree cover	4	-149661	299329.1	0.00	0.24	
	Curvature + Tree cover	5	-149660	299330.4	1.33	0.12	
	River + Tree cover	5	-149660	299330.7	1.62	0.10	
	Road + Tree cover	5	-149660	299330.8	1.72	0.10	
	Village + Tree cover	5	-149661	299331.1	1.98	0.09	
	Curvature + River + Tree cover	6	-149660	299332.0	2.94	0.05	
	Curvature + Road + Tree cover	6	-149660	299332.1	3.04	0.05	
	Curvature + Village + Tree cover	6	-149660	299332.4	3.31	0.05	
	River + Road + Tree cover	6	-149660	299332.6	3.47	0.04	
	River + Village + Tree cover	6	-149660	299332.7	3.61	0.04	
	Road +Village + Tree cover	6	-149660	299332.8	3.71	0.04	
	Night	River + Road + Tree cover	6	-151333	302677.2	0.00	0.23
		River + Tree cover	5	-151334	302678.1	0.96	0.14
		Curvature + River + Road + Tree cover	7	-151332	302678.7	1.55	0.11
River + Road + Village + Tree cover		7	-151333	302679.1	1.90	0.09	
Tree cover		4	-151336	302679.3	2.12	0.08	
Curvature + River + Tree cover		6	-151334	302679.7	2.52	0.06	
River + Village + Tree cover		6	-151334	302680.1	2.93	0.05	
Road + Tree cover		5	-151335	302680.5	3.36	0.04	



**Table S3 (Continued):** Model rankings according to AIC for hirola step selection functions (dry season).

<b>Time</b>	<b>Model variables</b>	<b>K</b>	<b>LL</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b><math>\omega_i</math></b>
	Curvature + River + Road + Village + Tree cover	8	-151332	302680.6	3.45	0.04
	Curvature + Tree cover	5	-151335	302680.9	3.71	0.04
	Village + Tree cover	5	-151336	302681.2	4.00	0.03

The models were fitted using a generalized linear mixed model and evaluated using maximum likelihood method for each variable where K is number of degrees of freedom, LL the log-likelihood, AIC the Akaike Information Criterion,  $\Delta$ AIC is the difference in AIC values and  $\omega_i$  is the weight. Only models with  $\Delta$ AIC  $\leq$  4.0 presented.

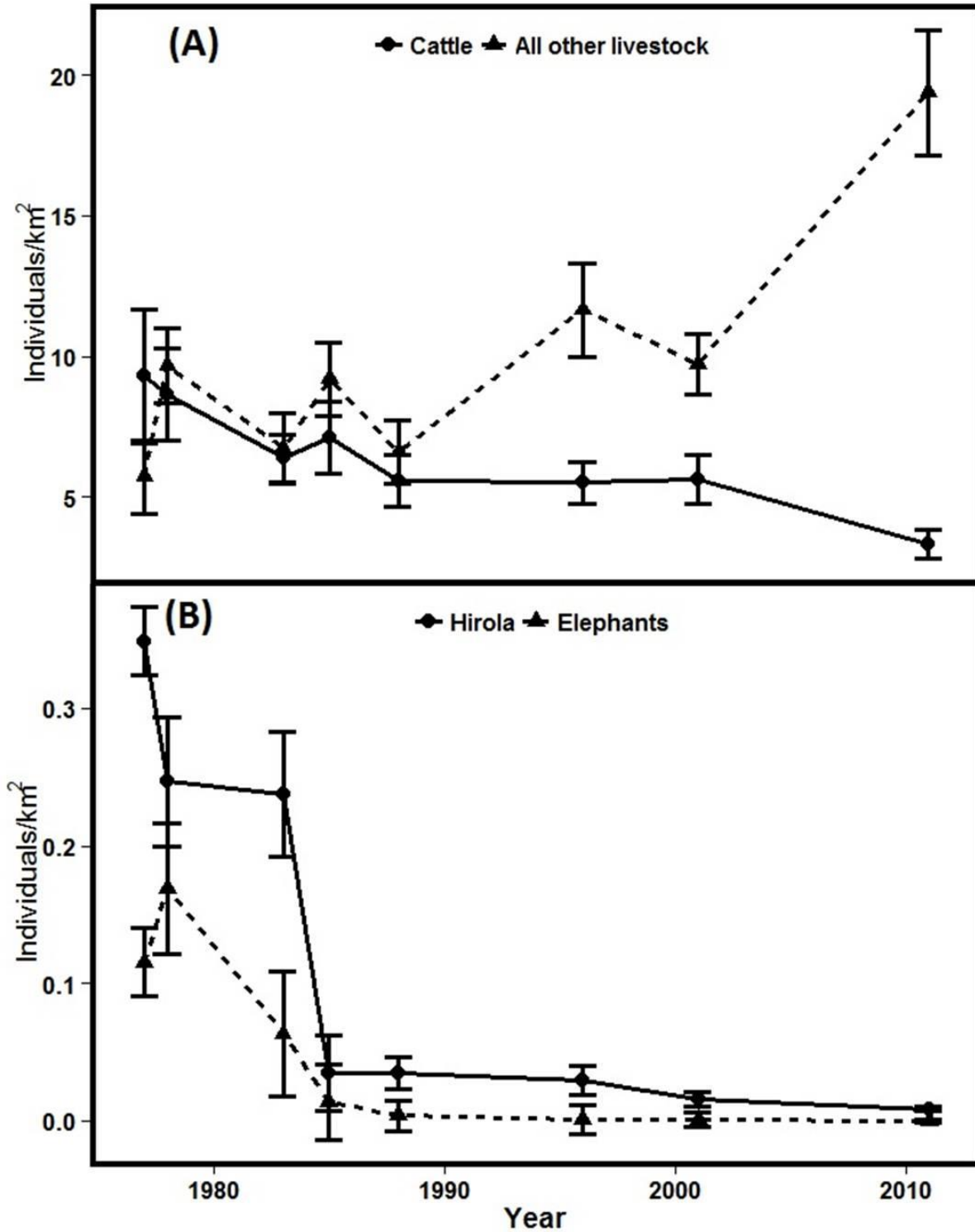
**Table S4:** Model rankings for hirola kill sites

<b>Model variables</b>	<b>K</b>	<b>LL</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>	<b><math>\omega_i</math></b>
River + Village + Tree cover	4	-84.7	177.6	0.00	0.33
River + Road + Village + Tree cover	5	-84.4	179.1	1.47	0.16
Curvature + River + Village + Tree cover	5	-84.4	179.1	1.48	0.16
River + Tree cover	3	-86.6	179.5	1.81	0.13
Curvature + River + Road + Village + Tree cover	6	-83.9	180.4	2.79	0.08
Curvature + River + Tree cover	4	-86.2	180.7	3.01	0.07
River + Road + Tree cover	4	-86.6	181.5	3.87	0.05

The models were fitted using a generalized linear mixed model and evaluated using maximum likelihood method for each variable where K is the number of degrees of freedom, LL the log-likelihood, AIC the Akaike Information Criterion,  $\Delta$ AIC is the difference in AIC values and  $\omega_i$  is the weight. Only models with  $\Delta$ AIC  $\leq$  4.0 presented.

Chapter 2 (Figures)

Figure S1. Estimates of livestock, hirola and elephant densities in Garissa County from 1977-2011. Data courtesy of Department of Remote Sensing and Resource Survey, Kenya.



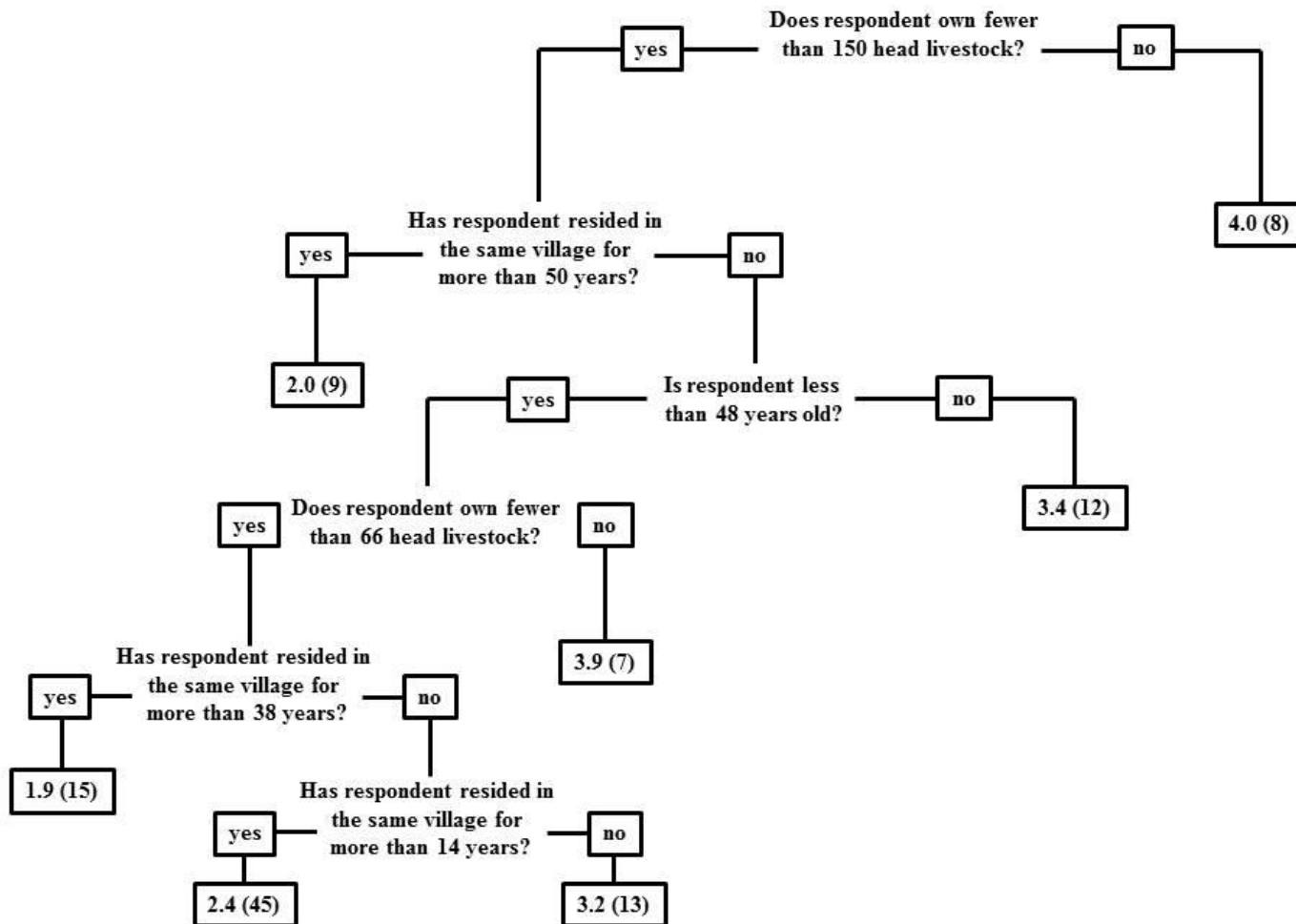
### Chapter 3 (Tables)

**Table S1.** Response frequencies to questions on range restoration solutions for improving hirola habitat in Ijara and Fafi subcounties (n = 131 respondents). Rangeland-restoration practices are ordered from least supported (Livestock reduction) to most supported (Elephant conservation).

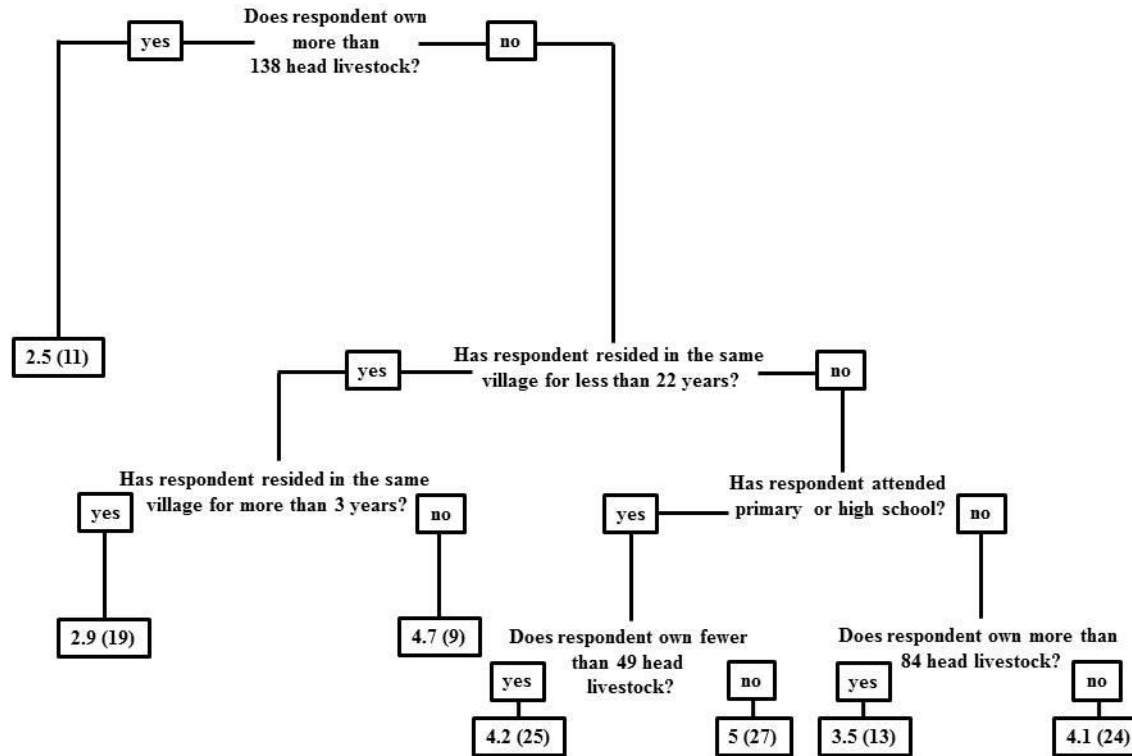
<b>Frequency (%) of responses to questions</b>							
<b>Response variable</b>	<b>Livestock reduction</b>	<b>Soil ripping</b>	<b>Controlled burning</b>	<b>Core area resting</b>	<b>Seeding and fertilization</b>	<b>Manual removal of trees</b>	<b>Elephant conservation</b>
<b>1. Strongly disagree</b>	44.3	30.5	43.5	22.1	16.8	2.3	4.6
<b>2. Disagree</b>	16.8	17.6	4.6	13	7.6	5.3	5.3
<b>3. Neutral</b>	1.5	12.9	8.4	8.1	3.1	6.9	3.8
<b>4. Agree</b>	33.6	27.5	30.5	46.6	7.6	68.7	69.5
<b>5. Strongly agree</b>	3.8	11.5	13	10.2	64.9	16.8	16.8
<b>In agreement</b>	37.4	39.0	43.5	56.8	72.5	85.5	86.3
<b>In disagreement</b>	61.1	48.1	48.1	35.1	24.4	7.6	9.9
<b>Neutral</b>	1.5	12.9	8.4	8.1	3.1	6.9	3.8

### Chapter 3 (Figures)

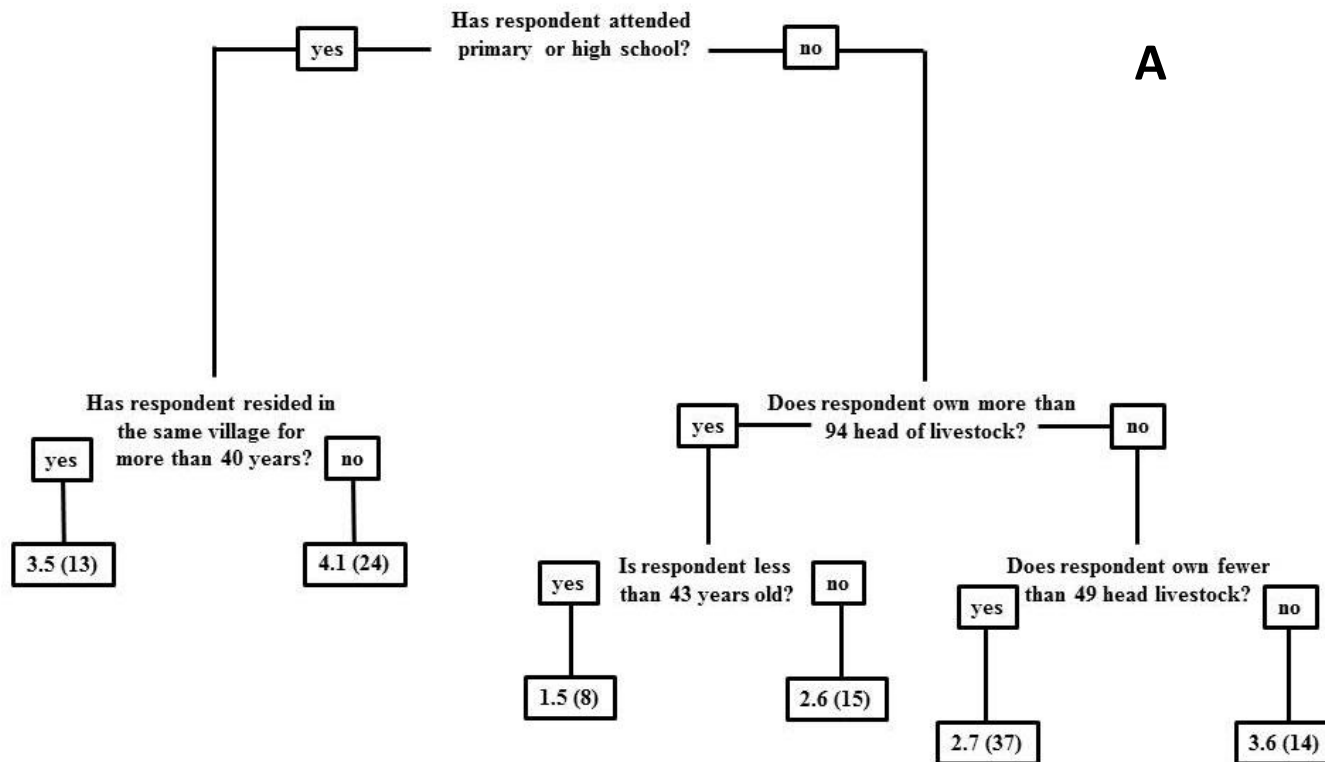
**Figure S1.** Optimal CART model for the question “Do you support controlled burning as a strategy to improve range quality?” Predictor variables are defined at each corresponding branch split. Terminal nodes represent the mean response (ranging from 1-5, where 1 represents the strongest level of disagreement, and 5 represents the strongest level of agreement); for each terminal node, numbers of respondents are included in parentheses. The branch lengths are proportional to the variance explained by the predictor variable at the split.



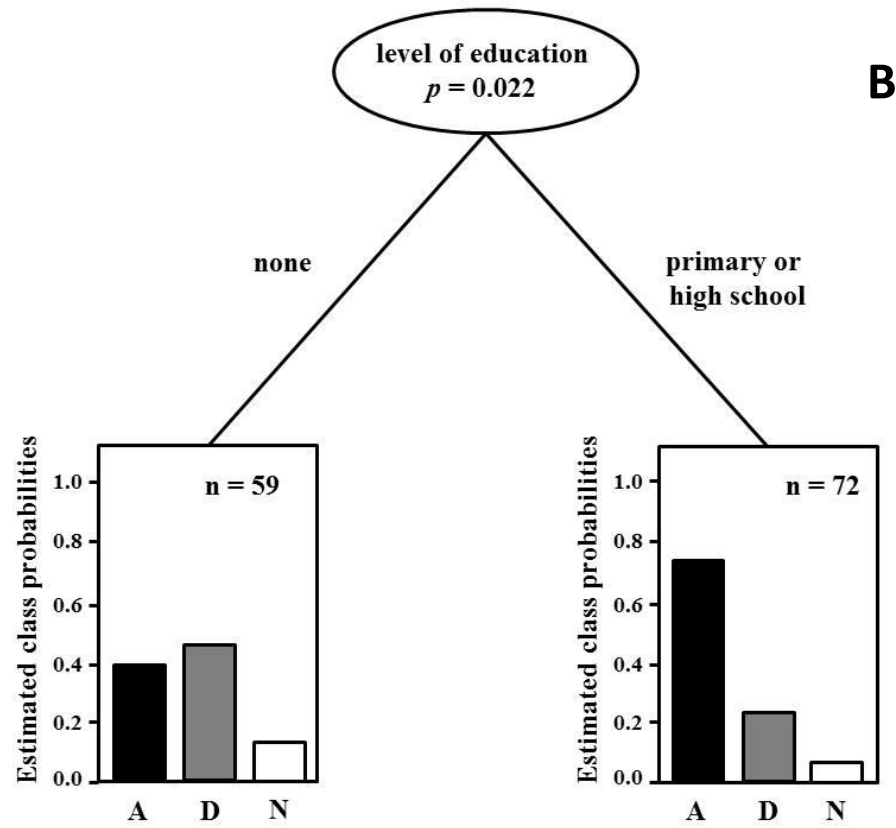
**Figure S2.** Optimal CART model for the question “Do you support manual removal of trees as a strategy to improve range quality?”.



**Figure S3.** (A) Optimal CART model for the question “Do you support rotational grazing as a strategy to improve range quality?”. (B) Conditional inference tree depicting the estimated probabilities and statistical significance of a social-demographic predictor for the same question. The prefixes A stand for Agree (those responding “Strongly agree” or “Agree” to the question), D for Disagree (those responding “Strongly disagree” or “Disagree”), and N for Neutral (those responding “Neutral” or “Undecided”).

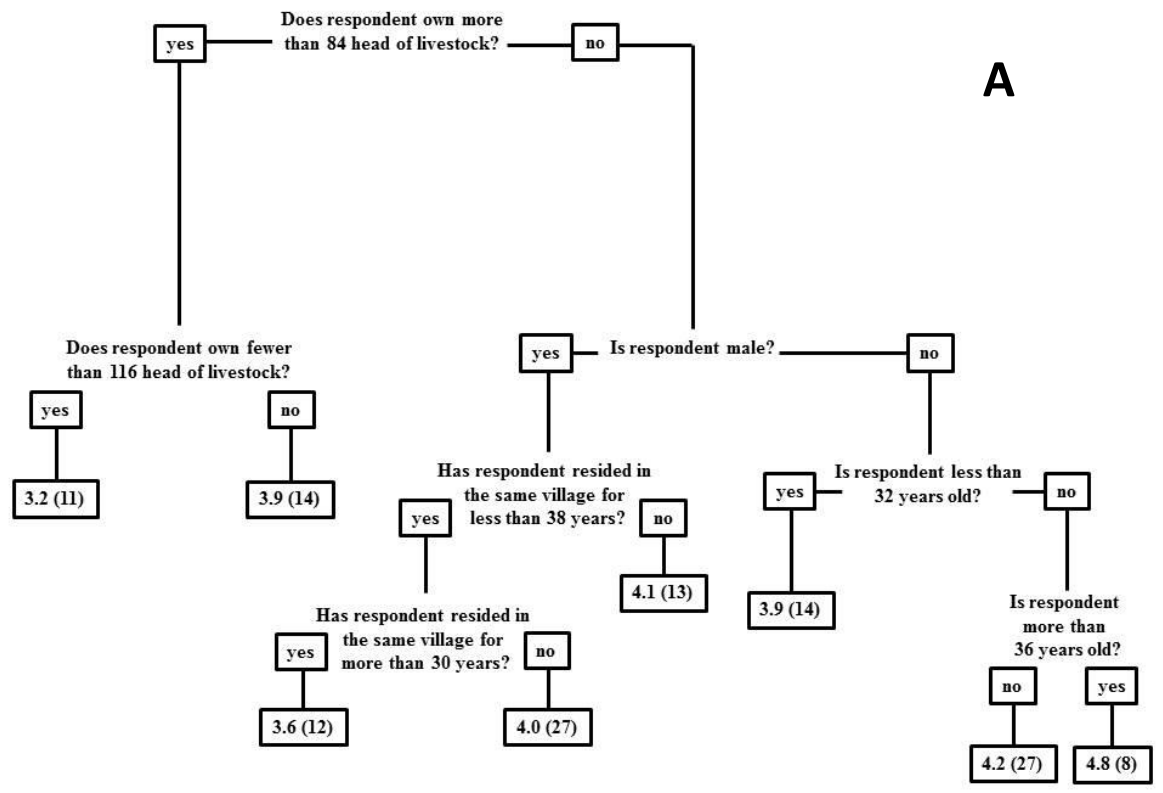


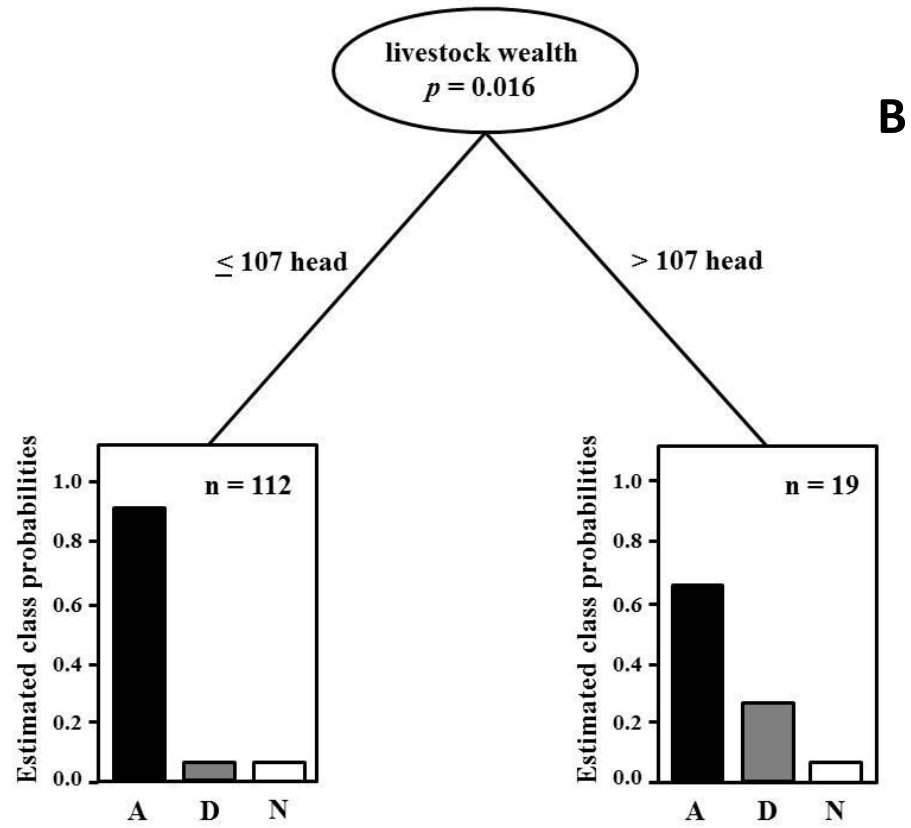




**B**

**Figure S4.** (A) Optimal CART model for the question “Do you support reseeding and fertilization as a strategy to improve range quality?”. (B) Conditional inference tree depicting the estimated probabilities and statistical significance of a social-demographic predictor for the same question. The prefixes A stand for Agree (those responding “Strongly agree” or “Agree” to the question), D for Disagree (those responding “Strongly disagree” or “Disagree”), and N for Neutral (those responding “Neutral” or “Undecided”).





**Figure S5.** Optimal CART model for the question “Do you support soil ripping as a strategy to improve range quality?”.

