

Resource selection and landscape change reveal mechanisms suppressing population recovery for the world's most endangered antelope

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Summary

1. Understanding how bottom-up and top-down forces affect resource selection can inform restoration efforts. With a global population size of < 500 individuals, the hirola *Beatragus hunteri* is the world's most endangered antelope, with a declining population since the 1970s. While the underlying mechanisms are unclear, some combination of habitat loss and predation are thought to be responsible for low abundances of contemporary populations.

2. Efforts to conserve hirola are hindered by a lack of understanding as to why population density remains low, despite eradication of the viral disease, rinderpest. To elucidate factors underlying chronically low numbers, we examined resource selection and landscape change within the hirola's native range. Because hirola are grazers, we hypothesized that the availability of open areas would be linked both to forage and safety from predators. We quantified: (i) changes in tree cover across the hirola's historical range in eastern Kenya over the past 27 years; (ii) how tree cover has influenced resource selection by hirola; and (iii) interactions between tree cover and predation.

3. Between 1985 and 2012, tree cover increased by 251% across the historical range of hirola. Tree encroachment was associated with a 98% decline of hirola and elephant *Loxodonta africana* populations, a 74% decline in cattle *Bos indicus*, an increase in browsing livestock by 327%, and a reduction in rainfall.

4. Although hirola avoided tree cover, we found no evidence that predation on hirola increased with increasing tree cover.

5. *Synthesis and applications.* Hirola may qualify as a refugee species, in which contemporary populations are restricted to suboptimal habitat and exhibit low survival, reproduction or both. The extinction of hirola would be the first of a mammalian genus on the African continent in modern history. We conclude that contemporary low numbers of hirola are due at least partly to habitat loss via tree encroachment, triggered by some combination of elephant extirpation, overgrazing, drought and perhaps fire suppression. We recommend a combination of rangeland restoration efforts (including conservation of elephants, manual clearing of trees, and grass seeding), increased enforcement of an existing protected area (Arawale National Reserve), and reintroductions to enhance recovery for this endangered species. These efforts will rely on enhanced support from the international conservation community and the cooperation of pastoralist communities with which the hirola coexist.

Key-words: *Beatragus hunteri*, elephant, endangered species, extinction, habitat loss, megaherbivore decline, predation risk, refugee species, reintroduction, tree encroachment

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Introduction

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; Thaler, McArt & Kaplan 2012). Consequently, understanding resource selection for species of conservation concern can inform recovery efforts, the design of protected areas, and predicted responses of animals to human disturbances (Johnson, Seip & Boyce 2004; Cañadas *et al.* 2005; Sawyer & Kauffman 2011; Selwood, McGeoch & Mac Nally 2014). Habitat loss can influence resource selection through reductions in food or birth sites (Sutherland 1996), or by increasing predation risk or poaching pressure (DeCesare *et al.* 2010). For example, industrial disturbances in western Canada have increased the abundance of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), thereby intensifying predation pressure on woodland caribou (*Rangifer tarandus caribou*; Wittmer, Sinclair & McLellan 2005). To counter these effects, caribou recovery guidelines have targeted a minimum of 65% of the landscape as undisturbed (Environment Canada 2012).

In African savannas, tree cover is regulated by a combination of fire, precipitation and herbivory (Scholes & Archer 1997; Sankaran *et al.* 2005; 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). Finally, the potential for tree encroachment to interact with predation risk and constrain abundance and distribution (Araujo & Luoto 2007; Soberón 2007) is particularly acute for savanna antelopes. For example, impala (*Aepyceros melampus*) are killed more frequently where tree cover is high, perceive these areas as risky, and thereby release palatable forage from herbivory (Ford *et al.* 2014). Elsewhere in Africa, ungulate communities are typified by a few numerically dominant species whose populations are regulated by resources, and several less-common species are controlled by predation (Sinclair 1985; Owen-Smith & Mason 2005; Georgiadis *et al.* 2007). Consequently, we might expect rare species of antelopes to be particularly sensitive to the interplay between predation and tree cover.

As the world's most endangered antelope, the hirola (*Beatragus hunteri*) has been declining since the 1970s (IUCN SSC Antelope Specialist Group 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 precise

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 (Ali 2016), 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. Had habitat loss or predation limited hirola before rinderpest, we would have expected a relatively rapid return to pre-outbreak population size (see also Sinclair, Mduma & Brashares 2003). Therefore, major questions remain as to why hirola have not rebounded in the 15 or more years since rinderpest eradication.

To elucidate the factors underlying chronically low numbers of hirola, we sought to link contemporary resource selection of hirola with sustained low population sizes. We addressed the following questions: (i) have hirola populations experienced habitat loss via tree encroachment since rinderpest eradication? and (ii) if tree encroachment has occurred, has this resulted in intensified predation pressure on hirola?

We expected that a combination of bottom-up (habitat loss via tree encroachment) and top-down (increased risk of predation following tree encroachment) forces would coincide with suppressed populations of hirola. Under the hypothesis of habitat loss, we predicted some combination of the following: (i) hirola would avoid tree cover; (ii) cattle (an obligate grazer with potential to compete with hirola, Butynski 2000) production would increase over the 30-year period that hirola have declined; (iii) elephants (an ecosystem engineer that facilitates understorey vegetation, Coverdale *et al.* 2016) would decline coincident with hirola-population declines; and (iv) rainfall—which may favour grasses over trees (Bond 2008)—would decline coincident with hirola-population declines. Under the hypothesis of increased risk of predation, we predicted that hirola would incur higher mortality with increasing tree cover, regardless of whether tree cover was avoided. Under both hypotheses, we expected tree cover to increase across the historical range of hirola. Additionally, we tested the hypothesis that hirola avoid people, which could indicate that low numbers of hirola are associated with human encroachment (e.g., roads, villages). We do not view these hypotheses or their associated predictions as mutually exclusive.

Materials and methods

STUDY AREA

We conducted our work in Garissa County, Kenya, 0°25'S, 40°32'E and ~80 m A.S.L. (Fig. 1a). This area is semi-arid (annual rainfall = 350–600 mm; Bunderson 1981), with rainfall occurring in two distinct seasons. The long rains occur in April to June, and the short rains occur in November to December.

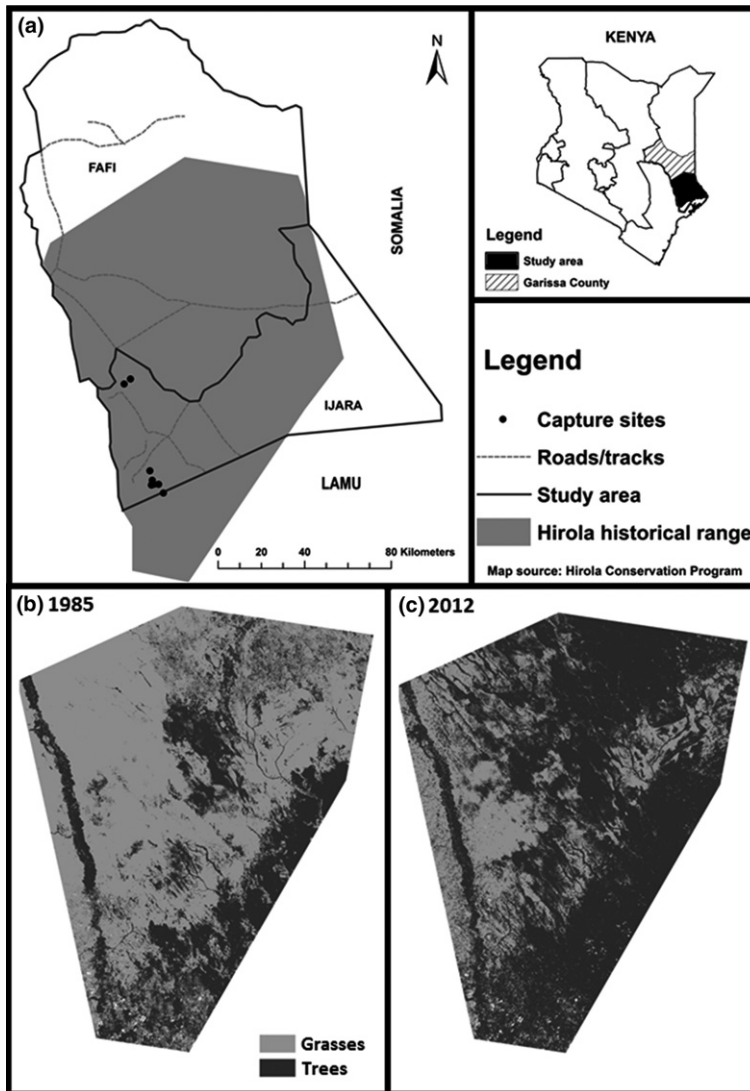


Fig. 1. (a) Study site in Garissa County, Kenya and the 1970s geographic range of hirola estimated from a minimum convex polygon based on historical records (Bunderson 1982; DRSRS 2012). (b) Tree cover across the hirola's historical range (1985). (c) Tree cover across the hirola's current range (2012). 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.

The average annual temperature is 30 °C, and it can exceed 36 °C during dry seasons.

The historical geographic range of hirola covered ~38 400 km² in eastern Kenya and southwestern Somalia (Butynski 2000). By the 1970s, however, hirola likely had been extirpated from Somalia, and persisted in a 17 000 km² area in eastern Kenya bounded by the Tana River to the west and the Boni Forest to the east (Butynski 2000). In 1977, the hirola's geographic range was assessed by aerial transects flown by the Kenya Department of Resource Surveys and Remote Sensing (DRSRS). The correspondence between these aerial surveys (DRSRS 2012) and ground surveys collected in the late 1970s (Bunderson 1981) surveys leads us to believe that we have accurately delineated the boundaries of the geographic range from the 1970s.

Both historically and currently, the majority of the hirola's range has been 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 were estimated to occur in the entire northeastern region of Kenya (Garissa, Mandera, and Wajir counties; Republic of Kenya 2010). Our study area falls within the Greater Horn of Africa biodiversity hotspot; here,

conservation for a multitude of endemic species is hampered by civil unrest (Hanson *et al.* 2009; 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 ellipsyprimmus*) and Kirk's dik-dik (*Madoqua kirkii*); plains zebra (*Equus burchelli*), buffalo (*Syncerus caffer*) and topi (*Damaliscus lunatus*) also are present. Large carnivores in the region include lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*) and African wild dogs (*Lycan pictus*).

DATA COLLECTION AND ANALYSIS

Quantifying tree encroachment within the hirola's historical range

We classified two remotely sensed images acquired in 1985 (Landsat 5) and 2012 (Landsat ETM+7). We used images taken during the dry season to distinguish understory vegetation from tree cover; spectral reflectance of tree leaves is significantly higher

than that of grass leaves during dry periods (Archibald & Scholes 2007; Goheen & Palmer 2010). We 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). We 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). We 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.

For ETM+7 images that exhibited the scan-alignment issue (acquired after May 2003), we applied a gap-filling algorithm in ENVI 5.0 (Chen *et al.* 2011). To train the model, we 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, we reclassified clouds and shadows into "no data" using ArcGIS, such that we were left with two classes in the image: tree cover and non-tree cover. Given the abundance of cloud cover over our study area, we combined multiple images (Table S1, Supporting Information) for each time step, to iteratively fill in the 'no data' classes created by cloud and shadow. Each of our two time steps (1985 and 2012) required four images to account for cloud cover. This allowed us to develop a single cloud-free image in which we filled missing data with values from corresponding images with a similar acquisition date (Wijedasa *et al.* 2012). To validate our model fit, we used Out-Of-Bag error (Evans & Cushman 2009). Additionally, abundances of hirola and elephants in the hirola's historical geographic range were assessed by aerial transects flown by the DRSRS (DRSRS 2012; Appendix S1, Fig. S1). Over a comparable period (1977–2011) to that elapsed between image classification, rainfall and drought severity were assessed by analysis of long-term (39-year) rainfall data (Appendix S2, Fig. S2).

Hirola capture and collaring

Between August and December 2012, we immobilized nine adult females from seven herds (mean herd size = 7.0 ± 2.0 SE, range = 5–11) with 3 mg Etorphine hydrochloride from a Bell 206 helicopter. We injected 30 mg Azaperone (Stresnil®; a tranquilizer, Kyron Laboratories (Pty) Limited, Johannesburg, South Africa) intravenously to increase depth of sedation and minimize stress on the captured individuals. 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, Berlin, Germany) before using 6 mg Diprenorphine hydrochloride as a reversal. Within 2 min 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 (i) relocated and re-sighted the nine individuals along with their respective herds once per month; and (ii) 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), we interpreted the individual movements as indicative of movements of the entire herd.

Development of step selection functions

We collected hourly GPS fixes from individuals from August 2012 to October 2015. To model habitat selection, we 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) that were associated with each observed step. We 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.

We 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). We developed separate models for day and night, and for wet and dry seasons. We also suspected that shifts in resource selection might occur throughout the day because (i) predators are most active at night; (ii) humans are least active at night; and (iii) thermal stress is lowest at night. We used model selection procedures to determine which landscape variable or combination of landscape variables best predicted habitat selection. We used AIC to rank models (Burnham & Anderson 2002), and present averaged coefficients for models $\Delta AIC_c < 4$ (Tables S2 and S3).

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), we compared tree cover in current (2012; c. 1000 km²) and historical (1985; c. 17 000 km²) geographic ranges of hirola. If tree cover has increased during the period of hirola decline, it may be indicative of habitat loss. However, we 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 regional changes in tree cover would not allow us 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, we 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. We 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 and shapes, we quantified the 95% isopleths of the utilization distribution from the seven GPS-

collared individuals associated with independent herds using the tracking data from 2012 to 2015. To create the utilization distributions, we used a kernel density estimator with a least-squares cross-validation smoother. The mean dimensions of wet season home ranges (width = 3858 ± 342 m SEM; length = $10\,505 \pm 1466$ m SEM) were smaller than dry season home ranges (width = 4461 ± 972 m SEM; length = $13\,743 \pm 2854$ m SEM). Using these dimensions, we 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 dimensions of potential home ranges. These grids resulted in 228 dry season potential home ranges and 361 wet season potential home ranges within the historical geographic range of hirola. We 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. We then used a paired *t*-test to test for differences in tree cover between 1985 and 2012, replicated over the potential home ranges.

Link between tree encroachment, predation, and movements

Although we lacked data to test an exhaustive list of mechanisms underlying the correlation between tree cover and hirola abundance, we did test the hypothesis that predation pressure had increased with tree encroachment. Between 2007 and 2015, local scouts opportunistically recorded the locations of sites where hirola were killed (hereafter 'kill sites') using handheld GPS units. Scouts identified kill sites in both open and tree cover areas. Over this 9-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%).

We 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 probability of predation. To create the RSF, we constructed a

minimum convex polygon (MCP) around all kill sites and used GIS software to sample an equal number of random locations ($n = 59$) within the MCP (765 km^2). We then used logistic regression (1 = observed, 0 = available) to estimate RSF coefficients (Manly *et al.* 2002). We used AIC to rank kill site RSF models, and present averaged coefficients for models $\Delta\text{AICc} < 4$ (Table S4).

Because the distribution of hirola inevitably constrains the distribution of kill sites, we 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 or non-tree cover) to the proportion of GPS fixes observed within that same habitat. When $\text{PCR} \approx 1$, 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 $\text{PCR} > 1$ for tree cover, and tree cover has increased since 1985, predation risk may have also increased for hirola. We 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 we 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 increased between 1985 and 2012 in our study area (C. Musyoki, pers. comm.).

Results

Within the historical geographic range of hirola, tree cover increased by 251% between 1985 and 2012 (Fig. 1). Increased tree cover was associated with declines in cattle (Fig. S1a) and elephants (Fig. S1b), increases in browsing livestock (Fig. S1a), decreased annual rainfall (Fig. S2a), and increased drought severity (Fig. S2b). Home ranges of hirola averaged $40.2 \pm 6.0 \text{ km}^2$ SEM in the wet season and $74.4 \pm 30.7 \text{ km}^2$ in the dry season (Table 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

Table 1. Summary of hirola home range sizes and the proportions of tree cover

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

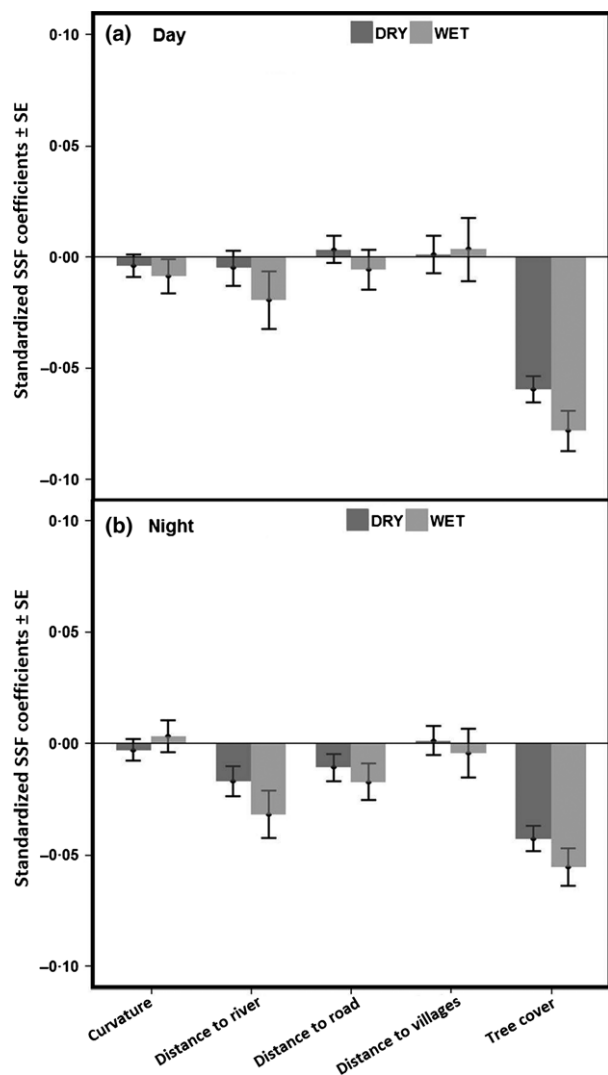


Fig. 2. Step selection function (SSF) coefficients for the strength of avoidance of landscape variables in (a) day and (b) night by hirola during dry and wet seasons. Note that 'river', 'road', and 'villages' are distance variables, such that a negative coefficient indicates selection for the corresponding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

cover has increased significantly between 1985 and 2012 ($P < 0.0001$), resulting in the loss of 43–53% of potentially suitable home ranges.

Step-selection functions demonstrated that hirola consistently avoided tree cover in all seasons (wet and dry) and times (day and night, Fig. 2). Results of the kill-site RSF suggest that kill sites were more likely to occur near villages, near roads, and in areas with convex curvature (Fig. 3). Tree cover was a poor predictor of kill sites. Similarly, the average *per capita* risk of mortality was 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.

Discussion

We quantified habitat loss and resource selection for hirola in eastern Kenya to elucidate the factors underlying

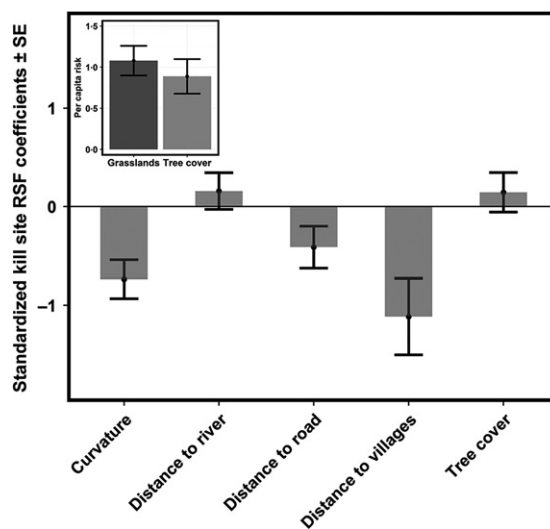


Fig. 3. Resource selection function (RSF) coefficients for hirola kill sites showing risk of mortality from predation as a function of landscape variables. A positive RSF coefficient indicates a higher than expected chance that a kill site will occur at a location compared to a random location. Note 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 grasslands and tree-cover areas.

suppressed populations of hirola. Our findings indicate that there was a 251% increase in tree cover between 1985 and 2012, suggesting that contemporary low numbers of hirola are due largely to habitat loss via tree encroachment. Below, we first entertain factors that potentially underlied tree encroachment, and then consider alternative hypotheses as to why hirola populations failed to recover following rinderpest eradication. These hypotheses ultimately fall into two non-exclusive categories: bottom-up and top-down forcing.

Why did tree cover increase so markedly over the past three decades? First, overgrazing by livestock may have reduced grasslands and increased tree cover (du Toit & Cumming 1999). The Kenya DRSRS has documented an increase in goats, camels and sheep coincident with a decline in cattle, during which tree encroachment occurred (Fig. S1). In eastern Kenya, most land is utilized for livestock production by nomadic communities. 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 the interpretation that lack of hirola recovery and declining cattle production are rooted in the loss of grasslands on which both species rely, although it is unclear whether overgrazing by cattle contributed to tree encroachment. Additionally, the cattle that remain in Garissa County may be sufficient to limit population recovery of hirola, although we believe this hypothesis is implausible because hirola are attracted to both roads and villages—centres of human activity where cattle

numbers are higher (Fig. 2). The extent to which cattle competitively suppress hirola populations remains a major question, and one which we hope to address experimentally with large-scale, voluntary livestock reduction (A.H. Ali, R. Amin, J.S. Evans, A.T. Ford, M. Fischer, A. Kibara, & J.R. Goheen, unpublished data).

Second, elephant extirpation may have fuelled tree encroachment and subsequent reduction in grasslands. Elephants browse, uproot and kill trees, thereby reducing tree cover in many African savannas (Owen-Smith 1989; Daskin, Stalmans & Pringle 2016; Morrison, Holdo & Anderson 2016). Consequently, hirola could be exhibiting a secondary extinction debt (*sensu* Brodie *et al.* 2014) in which tree encroachment stemming from elephant extirpation has predisposed hirola to high risk of extinction.

Third, drying conditions may favour trees at the expense of grasses (Bond 2008; February *et al.* 2013), and drought has increased in our study area over the past 40 years. Additionally, reduced grass cover can be associated with decreased fire frequency (Archer *et al.* 1988), and fire suppression may in turn have led to tree encroachment. Although we lack data on historical fire regimes, traditional use of fire in eastern Kenya was discouraged by the government since 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 (A. Diis, Ministry of Livestock, Kenya, pers. comm.).

Our kill-site analyses strengthen the interpretation that tree encroachment has impacted hirola primarily via loss of forage. The *per capita* risk of mortality did not change with tree cover, suggesting that tree encroachment likely is influencing hirola populations primarily through bottom-up pathways. Alternatively, it is possible that other more common, grass-dependent ungulates (plains zebra, buffalo) increasingly have been “compressed” into smaller patches of grassland, thereby concentrating hunting by predators in the ever-shrinking habitats suitable for hirola. Such apparent competition structures other ungulate communities (e.g., McLoughlin & Owen-Smith 2003; Georgiadis *et al.* 2007; Chirima *et al.* 2012), and remains a hypothesis open for testing in our system. Although we lack data on predator abundance, a close relative of hirola in our study area (the coastal topi, *D. lunatus* ssp. *topi*) exhibited comparable declines to those of hirola in the 1980s but has since rebounded following rinderpest eradication (Butynski 2000). This suggests that predation on topi has not increased over time, and we 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 (Butynski 2000).

In addition to predation, disease (other than the eradicated rinderpest virus, i.e., bovine tuberculosis and anthrax) may further suppress population recovery of hirola. Although we did not quantify disease prevalence directly, no antibodies for these diseases were found from

blood screening of individuals captured in our study (I. Lekool, Kenya Wildlife Service veterinarian, pers. comm.) or in individuals in a translocation in the late 1990s (Butynski 2000). In sum, and although we cannot rule out the potential roles of predation and disease in suppressing hirola recovery, we found no evidence for top-down forcing in our research.

Historically, hirola have been confined to open grasslands east of the Tana River in Kenya into southwestern Somalia, where they are thought to have persisted because of competitive release with their closest living relative, hartebeest (*Alcelaphus* spp, which does not occur east of the Tana; Kingdon 1982). Although we do not report on vital rates of individuals, hirola may qualify as a refugee species (*sensu* Kerley, Kowalczyk & Cormsigt 2012), in which small populations occur solely in suboptimal habitat and thus exhibit decreased fitness. Even without such extraneous factors as habitat loss, small-ranged species like hirola are at greater risk of succumbing to demographic and genetic stochasticity (Caughley 1994; see also the case of the extinct blue antelope, *Hippotragus leucophaeus* in South Africa, detailed in Kerley *et al.* 2009). Antelopes (Payne & Bro-Jørgensen 2016) and other taxa (Thuiller, Lavorel & Araujo 2005; Pearson *et al.* 2014) with small geographic ranges are at greater risk of extinction stemming from climate change, which is predicted to be especially pronounced in the Horn of Africa (Niang *et al.* 2014), and which manifests in our study system as decreased rainfall. This has led to calls for the creation of new protected areas, stronger enforcement of existing protected areas, and establishment of captive populations to serve as a source for future reintroductions (e.g., Payne & Bro-Jørgensen 2016). Along these lines, we advocate strongly for the re-instatement of Arawale National Reserve and other areas identified as critical habitat in eastern Kenya (Butynski 2000). In the mid 1970s, Arawale was identified as habitat critical for hirola conservation, but enforcement of Arawale as a protected area deteriorated due to financial constraints in the mid-1980s. As a result, Kenya (and the rest of the world) lost the only formally protected area dedicated to the conservation of hirola.

Hirola are the only extant members of the once-wide-spread genus *Beatragus*, the most ancestral of alcelaphine antelopes. Coupled with its critically endangered status, the phylogenetic distinctiveness of this species has led to its inclusion as a ‘Top 100’ Evolutionarily Distinct and Globally Endangered (EDGE) mammal in dire need of enhanced conservation attention (Isaac *et al.* 2007). Unless current conservation efforts are intensified and populations increase, the hirola is unenviably poised to constitute the first extinction of a mammalian genus during historic times in mainland Africa (IUCN SSC Antelope Specialist Group 2008). We conclude that some combination of elephant extirpation, overgrazing, drought, and perhaps fire suppression likely drove tree encroachment in eastern Kenya, which has impeded hirola recovery following rinderpest eradication. Regardless of the precise mechanism(s),

habitat restoration within the historical geographic range of hirola is a prerequisite to their recovery, and to ensure that hirola are not relegated to a 'put and take' strategy in which reintroduced individuals stand little chance of survival and reproduction. Our work provides scientific justification to national agencies and non-government 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. Given the results presented here, we recommend a combination of range restoration efforts alongside the re-instatement of Arawale National Reserve to enhance the recovery of hirola. A parallel effort to the current study (A.H. Ali, M.J. Kauffman, R. Amin, D. Mallon & J.R. Goheen, unpublished data) has quantified acceptance of several habitat-restoration practices—including elephant conservation, manual tree removal, grass reseeding and voluntary reduction in livestock—to guide our team's future efforts and maximize the chances that hirola conservation will be successful over the long-term.

Authors' contributions

A.H.A., D.J.M., J.K., R.A. and J.R.G. conceived of the study; A.H.A. and J.R.G. designed and performed the study; A.H.A., A.T.F. and M.M.H. implemented S.S.F., R.S.F., and kill-site analyses; A.H.A. and J.S.E. analysed remotely sensed data; A.H.A. and J.R.G. drafted the manuscript; all authors contributed edits and insights.

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Data accessibility

Data are available from the Dryad Digital Repository, <https://doi.org/10.5061/dryad.p1v07> (Ali *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Livestock and elephant abundance in the historical geographic range of hirola.

Appendix S2. Rainfall in the historical geographic range of hirola.

Fig. S1. Livestock, elephant and hirola numbers in eastern Kenya, 1977–2011.

Fig. S2. Rainfall and drought in Ijara subcounty, 1970–2009.

Table S1. Landsat scenes used in classified image composites.

Table S2. Model rankings for step selection functions during the wet season.

Table S3. Model rankings for step selection functions during the dry season.

Table S4. Model rankings for hirola kill sites.