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Demographic drivers of a refugee species: large-scale experiments guide strategies for reintroductions of hirola

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Abstract. Effective reintroduction strategies require accurate estimates of vital rates and the factors that influence them. The hirola (*Beatragus hunteri*) is the rarest antelope on Earth, with a global population size of <500 individuals restricted to the Kenya–Somali border. We estimated vital rates of hirola populations exposed to varying levels of predation and rangeland quality from 2012 to 2015, and then built population matrices to estimate the finite rate of population change (λ) and demographic sensitivities. Mean survival for all age classes and population growth was highest in the low-predation–high-rangeland-quality setting ($\lambda = 1.08 \pm 0.03$ [mean $\pm$ SE]), and lowest in the high-predation–low-rangeland-quality setting ($\lambda = 0.70 \pm 0.22$). Retrospective demographic analyses revealed that increased fecundity (the number of female calves born to adult females annually) and female calf survival were responsible for higher population growth where large carnivores were absent. In contrast, variation in adult female survival was the primary contributor to differences in population growth attributable to rangeland quality. Our analyses suggest that hirola demography is driven by a combination of top-down (predation) and bottom-up (rangeland quality) forces, with populations in the contemporary geographic range impacted both by declining rangeland quality and predation. To enhance the chances of successful reintroductions, conservationists can consider rangeland restoration to boost both the survival and fecundity of adult females within the hirola's historical range.

Key words: endangered species; habitat quality; life table response experiment; predation; rangeland; recruitment; survival; ungulate; vital rate.

Introduction

A species' geographic range can be viewed as a proxy of its realized niche, in which a combination of factors (e.g., resource availability, predation, interspecific competition) combine to influence vital rates and subsequent population growth. Species exhibiting rapid range collapse may be confined to habitats in which low rates of survival, recruitment, or both prevent positive population growth (Pulliam and Danielson 1991, Caughley 1994). For such "refugee species" (sensu Kerley et al. 2012), there is strong risk of conflating persistence within a habitat to suitability of that habitat, thereby obfuscating the efforts most likely to lead to recovery (Van Horne 1983, Lea et al. 2016).

The forces that affect wildlife populations, and thus extirpation and eventual extinction, encompass bottom-up and top-down processes that are dynamic in space and through time. Understanding ecological processes can be used to identify refugee species, thereby steering conservation efforts (Sinclair and Krebs 2002, Wallach et al. 2015). Nevertheless, recovery efforts often are conducted without an a priori understanding of the relative roles of these ecological processes, glossing over the possibility that species may currently exist as refugees and leading to ineffective reintroductions in suboptimal habitats (Balmford and Cowling 2006, Tanentzap et al. 2012, Morrison 2013). While the escalation of extinction

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risk has led to heightened urgency to identify effective conservation strategies, many efforts still fail to incorporate evidence-based practices that could increase their impact (Sutherland et al. 2004). Experimental approaches can inform the degree to which populations are limited top-down, bottom-up, or both; for example, Armstrong and Perrott (2000) and Armstrong et al. (2002) combined food supplementation with stochastic simulation models to demonstrate that Stitchbird (*Notiomystis cincta*) reintroductions were limited by food on predator-free islands. In light of the widening gap between conservation efforts and continued declines in populations, the scientific community increasingly is emphasizing the importance of evidence, experimental or otherwise, to ground management interventions for species of conservation concern in the most rigorous science possible (Beale et al. 2013, Tulloch et al. 2015).

The hirola antelope (*Beatragus hunteri*) is a critically endangered species from a once-widespread lineage. Hirola declined from over 15,000 individuals in the 1960s to <500 individuals today (IUCN 2008), most precipitously in the 1980s following a rinderpest outbreak, such that their geographic range has contracted to a narrow swath of rangeland between the Tana River and the Boni Forest. However, following eradication of rinderpest by 2001 (Mariner et al. 2012), hirola populations did not recover to pre-outbreak levels (Ali et al. 2017, Fig. 1). Our recent work has demonstrated that range degradation, through tree encroachment, may underlie continued suppression of hirola populations (Ali et al. 2017). Additionally, some have speculated that a combination of heightened predation and reduced rangeland quality are responsible for its current status 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 and Barbault 1996, Sutherland et al. 2004, Armstrong and Seddon 2008). Recovery efforts for hirola have occurred mostly through community-based conservancies and sanctuaries (e.g., the Ishaqbini Community Conservancy in eastern Kenya; Measham and Lumbasi 2013), because the vast majority (>90%) of hirola occur outside formally protected areas alongside pastoralists and their livestock.

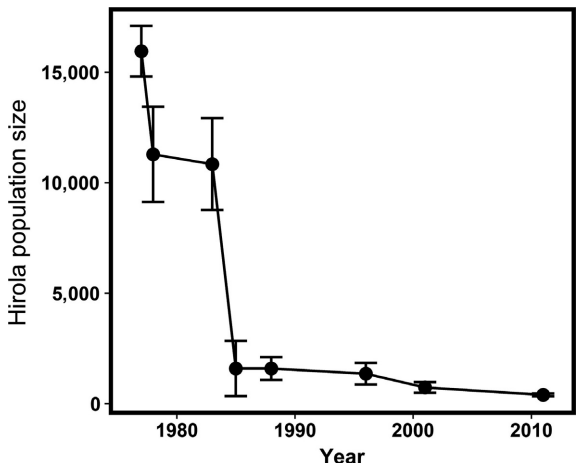

FIG. 1. Estimated hirola population trends from 1977–2011 (mean ± SE). The population crash in the mid-1980s is the result of a rinderpest outbreak in the Horn of Africa. Data courtesy of the Kenya Department of Resource Surveys and Remote Sensing. See Appendix S1 for methods for aerial surveys.

Vital rates entail the survival, growth, and reproduction of individuals, and responses of these vital rates to environmental conditions therefore determine population dynamics. We sought to quantify the relative importance of age-specific survival and fecundity to population growth of hirola, with the intent of centering recovery plans on the processes most likely to reverse population declines (Johnson et al. 2010). Between 2012 and 2015, we quantified vital rates under three ecological conditions: (1) a predator-proof sanctuary with relatively high rangeland quality because of minimal livestock grazing (hereafter "sanctuary"), nested within the broader 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 conservancy (hereafter "rangelands") with similar numbers of large carnivores to the conservancy (Appendix S1: Table S1), but with lower rangeland quality (due to high levels of livestock grazing that reduced forage availability). Our study provides a rare example of how large-scale experiments can be used to understand species declines and guide reintroduction efforts for a critically endangered species (see also Saltz and Rubenstein 1995, Sarrazin and Legendre 2000, and Steury and Murray 2004). This is especially important considering that hirola are restricted to the Kenya–Somalia border, a remote and volatile area where wildlife populations are difficult to monitor.

Materials and Methods

Study area

We 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 (Appendix S1: Fig. S1). Ijara is one of the driest regions in Kenya with an average annual rainfall ranging from 350–550 mm. Xeric conditions are ideal for hirola, which thrive in open, semiarid grasslands (Kingdon 1982). Livestock production is the most common land use in the region and includes production of domestic goat (*Capra hircus*), sheep (*Ovis aries*), cattle (*Bos indicus*), camel (*Camelus dromedarius*), and donkey (*Equus asinus*). Native species of large carnivores include 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 rangelands (Appendix S1: Table S1).

Demographic study design

Environmental setting 1: sanctuary.—In August 2012, a 25-km^2 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 in an effort to curtail ongoing hirola declines (Appendix S1: Fig. S1). The sanctuary fence is 2.5 m tall with electrified (6,000–7,000 V) strands of wires spaced at 30 cm with wire mesh along the lower 1.5-m section. Dedicated personnel maintain the fence and patrol the sanctuary on a daily basis. Prior to translocating hirola into the sanctuary, we removed livestock and large carnivores (six spotted hyenas and six cheetahs), and established three permanent rain-catchment troughs. We then translocated hirola from the outskirts of Ishaqbini Community Conservancy into the sanctuary. We used a combination of helicopter drives and net capture; additionally, 12 individuals were enclosed within the sanctuary at the time of construction for a total of 48 individuals (i.e., ~10% of the global population; 5 males, 39 females, and 4 calves; King et al. 2011). 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. Individuals settled into six distinct groups after the first six months and maintained this social structure throughout the study period (2012–2015). The sex and age composition of the enclosed herd approximated the social structure and densities reported for hirola throughout their geographic ranges (Andanje 2002).

Environmental setting 2: conservancy.—Located on the eastern bank of the Tana River in Kenya and with an area of 240 km^2, the Ishaqbini Community Conservancy (1°54′19.56″ S, 40°12′49.89″ E; Appendix S1: Fig. S1) was established in 2005 by Terra Nuova (an Italian nongovernment organization for conservation and rural development; Njoroge et al. 2015). In an attempt to improve rangeland quality for hirola and other wildlife, livestock grazing has been minimized since 2008, thereby providing more grass biomass relative to rangelands (Appendix S1: Fig. S2). About six hirola groups use the conservancy at varying times of the year. We restricted our analyses to 38 individuals (slightly lower than the ~10% of the global population; King et al. 2011) in three resident groups that occupied the conservancy for the duration of our study. Hirola have stable groups and are faithful to particular areas, so we were able to identify 38 unique individuals throughout the year using natural marks including ear nicks, horn size and shape, scars, and coloration (see also Bro-Jørgensen and Durant 2003).

Environmental setting 3: rangelands.—From August 2012 to December 2012, we deployed GPS PLUS collars (Vectronic Aerospace, Berlin, Germany) on nine adult females from seven different groups (group size = 7.0 ± 2.0 [mean ± SE], range = 5–11; ~15% of the global population) spread in a 1,000 km^2 area outside the conservancy and the sanctuary (Appendix S1: Fig. S1). GPS collars allowed us to relocate the seven groups weekly 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 (see *Environmental setting 1: sanctuary*). The rangelands were characterized by lower grass biomass due to intensive livestock grazing (Appendix S1: Fig. S2) and comparable abundances of large carnivores to conservancy lands (Appendix S1: Table S1). This third environmental setting is representative of the hirola's current 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.

Demographic data collection and analysis

We used weekly resightings of groups from all three settings to estimate age-specific survival rates of calves, female sub-adults, and adults, and fecundity of adult females (see below; Andanje 2002, Johnson et al. 2010). We summarized the weekly totals from re-sighting to generate an average monthly count of females per setting, which we used to develop Kaplan-Meier (KM) models and generate survival rates for every year for the entire experimental period (3 yr). During each survey, we identified all observed individuals and searched for any missing individuals that were counted in the previous survey(s) for a period of up to two weeks. Searching for missing individuals entailed intensive bouts of searching, during which we covered a 7–12 km radius in concentric circles from the centroid at which we detected the rest of the group. Following these counts, and in light of the high fidelity and cohesion of individuals within groups (Andanje 2002), we interpreted any missing individuals as evidence of mortality. Subsequently, and toward the last week of every month, we conducted a verification survey to validate our observed counts. Verifications involved a combination of Pearson correlations (Lawrence and Lin 1989), Brier scores (Brier 1950), and Cohen's weighted kappa methods (Cohen 1968) to quantify agreement between resighting by multiple observers (Appendix S1: Table S2).

Similar to other alcelaphine antelopes, the majority of adult 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). Hirola have 7–8 month gestation periods (Kingdon 1982), and we began noticing gravid females ~2–3 months before parturition. Therefore, we used a post-birth census to estimate adult fecundity, measured as the average proportion of adult females that gave birth to calves over each 12-month period. This proportion integrates three rates, none of which we measured directly (the probability of pregnancy, the probability of birth given pregnancy, and calf sex ratio), with a fourth rate, the litter size of hirola, which did not vary. Females give birth to a single calf at approximately 3 yr old and live up to 10 yr (Andanje 2002). We assumed a 50:50 sex ratio for all calves (we could not distinguish sexes of calves) in estimating female fecundities; this is typical for ungulates when sample sizes are large or when multi-year data is used (Raithel et al. 2007). Post-breeding censuses are used commonly for field studies that have logistical and other challenges (Cooch et al. 2003); this approach allowed us to count and employ sight–resight methods on adult females with calves, since calves often have reduced mobility and adult-female–calf pairs may temporarily disassociate from groups.

We used the survival package in R version 3.2 (R Core Team 2013, Therneau 2013) to generate mean cumulative survival rates for each age class per year (Kaplan and Meier 1958, White and Garrott 1990), and the popbio package (Stubben and Milligan 2007) to develop an age-structured matrix for each setting in each transition year (for a total of nine matrices). To implement matrix models, we followed Andanje (2002) in modeling hirola demography with three age classes (calves [i.e., individuals born within the monitoring year], female sub-adults between 1 and 2 yr old, and female adults >2 yr) to account for differences in survival and fecundity. Following Caswell (2001), we constructed a female-based post-birth model with a 1-yr projection interval using a 3 × 3 matrix

$$A = \begin{pmatrix} 0 & 0 & S_{ad} & F_{ad} \\ S_c & 0 & 0 & \\ 0 & S_{sa} & S_{ad} & \end{pmatrix} \begin{pmatrix} \text{Calves} \\ \text{Subadults} \\ \text{Adults} \end{pmatrix}$$

where each matrix element represents a vital rate for each of the classes (calves, sub-adults, and adults; Morris and Doak 2002) defined as S_c, survival of calves; S_{sa}, survival of sub-adults; S_{ad}, survival of adults; and F_{ad}, fecundity rate of adult females. At the beginning of each survey, we identified the proportion of individuals in each age class, and matched these with corresponding survival and fecundity rates.

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 matrices, we estimated the finite rate of population change (λ) as the dominant eigenvalue (Caswell 2001) and calculated the geometric means for each setting across all the three transition years (2012–2013, 2013–2014, 2014–2015). We plotted the KM estimates of annual survival and the cumulative hazard curves for all the age classes in the three settings (Appendix S1: Fig. S3). To account for uncertainty in model selection, we estimated the standard errors of estimates of population parameters by full-model averaging (Johnson and Omland 2004, Symonds and Moussalli 2011). From the model output, we extracted the coefficients, standard errors and associated degrees of freedom. We conducted a series of Z tests in R to evaluate differences in λ between pairs of environmental settings, and we calculated both analytical sensitivity and elasticity estimates for lower level vital rates across each environmental setting in the popbio package (Stubben and Milligan 2007).

We conducted a life table response experiment (LTRE) to decompose effects of environmental settings on λ into contributions from setting-specific vital rates (Bruna and Oli 2005, Barclay et al. 2011). LTRE analysis quantifies the real contributions of variation in vital rates to differences in λ between two or more populations (Horvitz et al. 1997). We calculated contributions from demographic matrices for the 2012–2015 period using averaged vital rates estimated from each population to facilitate pairwise (settings) comparisons (sanctuary vs. conservancy, sanctuary vs. rangelands, conservancy vs. rangelands). We calculated the change in λ between each paired *setting* as $\Delta\lambda = \lambda_i - \lambda_j$, which can also be estimated using

$$\sum_m (x_{m_i} - x_{m_j}) * s_{ij}$$

where $(x_{m_i} - x_{m_j})$ is the difference in vital rate m for a pair of settings, and s_{ij} is the mean sensitivity of λ to changes in vital rate m evaluated for a "mean" matrix (i.e., midway between the two matrices being compared) between the pair of settings being compared (Bruna and Oli 2005). Thus, each term in the summation represents the contribution of vital rate m to the Δλ arising between a pair of settings.

Results

We tracked telemetered hirola from the time they were fitted with GPS collars (between August and December 2012) through December 2015. Adult survival was generally higher than sub-adult and calf survival across all three settings and years, with survival rates highest in the sanctuary for all three age classes (Fig. 2). Of particular note were (1) increases in adult survival due to heightened rangeland quality (S_{ad} sanctuary ≈ S_{ad} conservancy > S_{ad} rangelands; Fig. 2A); (2) increases in sub-adult survival due to large carnivore exclusion (S_{sa} sanctuary > S_{sa} conservancy ≈ S_{sa} rangelands; Fig. 2B); (3) increases in calf survival due to large carnivore exclusion (S_c sanctuary > S_c conservancy ≈ S_c rangelands; Fig. 2C); and (4) increases in fecundity due to large carnivore exclusion (F_{ad} sanctuary > F_{ad} conservancy ≈ F_{ad} rangelands; Fig. 2D). Elasticity of adult survival was higher in the conservancy and rangelands

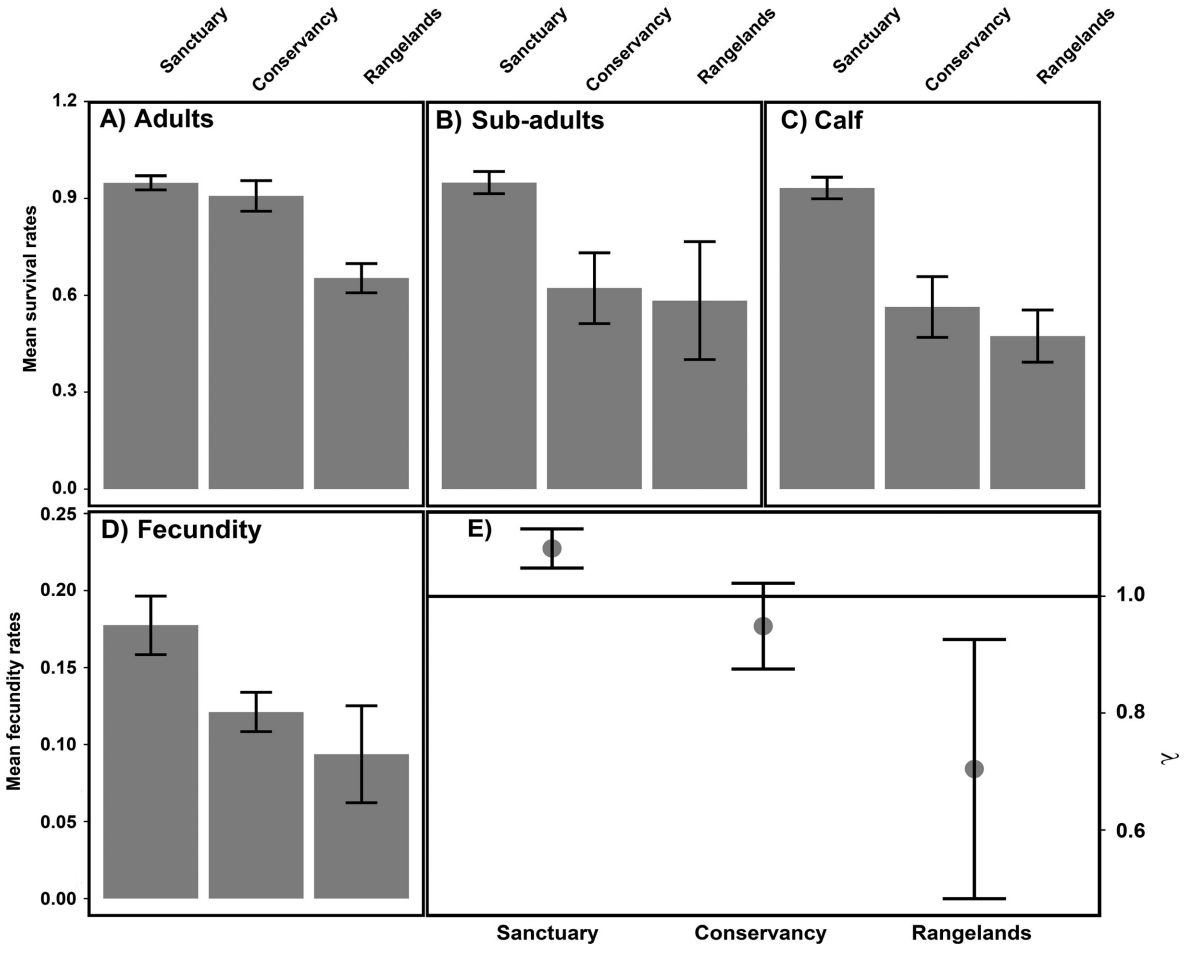

FIG. 2. Survival rates (mean ± SE) for hirola in the sanctuary, conservancy, and rangelands for (A) adult, (B) sub-adult, and (C) calf age classes from 2012–2015; (D) estimated adult fecundity rates (mean ± SE) of hirola in the sanctuary, conservancy, and rangelands from 2012–2015; and (E) estimated population growth rates (mean λ ± SE) of hirola in the sanctuary, conservancy, and rangelands.

TABLE 1. Differences in survival rates, adult fecundity, and sensitivities for age classes between pairs of settings from 2012–2015 study periods.

	Differences and range in vital rate			Sensitivity and range		
Age class	Sanctuary vs. Conservancy	Sanctuary vs. Rangelands	Conservancy vs. Rangelands	Sanctuary vs. Conservancy	Sanctuary vs. Rangelands	Conservancy vs. Rangelands
Survival						
Calf	**0.37 (0.20–0.60)**	**0.46 (0.19–0.80)**	0.09 (0.02–0.16)	0.09 (0.08–0.10)	0.09 (0.07–0.11)	0.07 (0.03–0.09)
Sub-adult	**0.33 (0.03–0.70)**	**0.37 (0.20–0.60)**	0.04 (−0.10–0.17)	0.09 (0.07–0.10)	0.09 (0.06–0.10)	0.06 (0.02–0.09)
Adult	0.04 (0.01–0.10)	**0.30 (0.10–0.63)**	**0.25 (0.11–0.53)**	0.86 (0.84–0.89)	0.86 (0.83–0.90)	0.91 (0.86–0.98)
Fecundity	**0.06 (0.05–0.10)**	**0.08 (0.02–0.12)**	0.03 (−0.03–0.06)	0.47 (0.38–0.58)	0.47 (0.36–0.57)	0.34 (0.08–0.54)

Notes: Values are means. Statistically significant differences ($P < 0.05$) between settings are shown in boldface type. The first environmental setting is the reference for the difference between pairs of environmental settings.

compared to the sanctuary (Appendix S1: Table S3). However, the mean sensitivities for sub-adult and calf survival in all three paired settings were statistically indistinguishable (Table 1).

The finite rate of population change (λ) of hirola was highest in the sanctuary (1.08 ± 0.03 [mean ± SE]), followed by the conservancy (0.95 ± 0.07) and the rangelands (0.70 ± 0.22; Fig. 2E). The finite rate of population change was higher in the sanctuary compared to the conservancy ($Z = 1.65$, $P < 0.05$; Fig. 2E), higher in the conservancy compared to the rangelands ($Z = 1.07$, $P = 0.05$; Fig. 2E), and higher

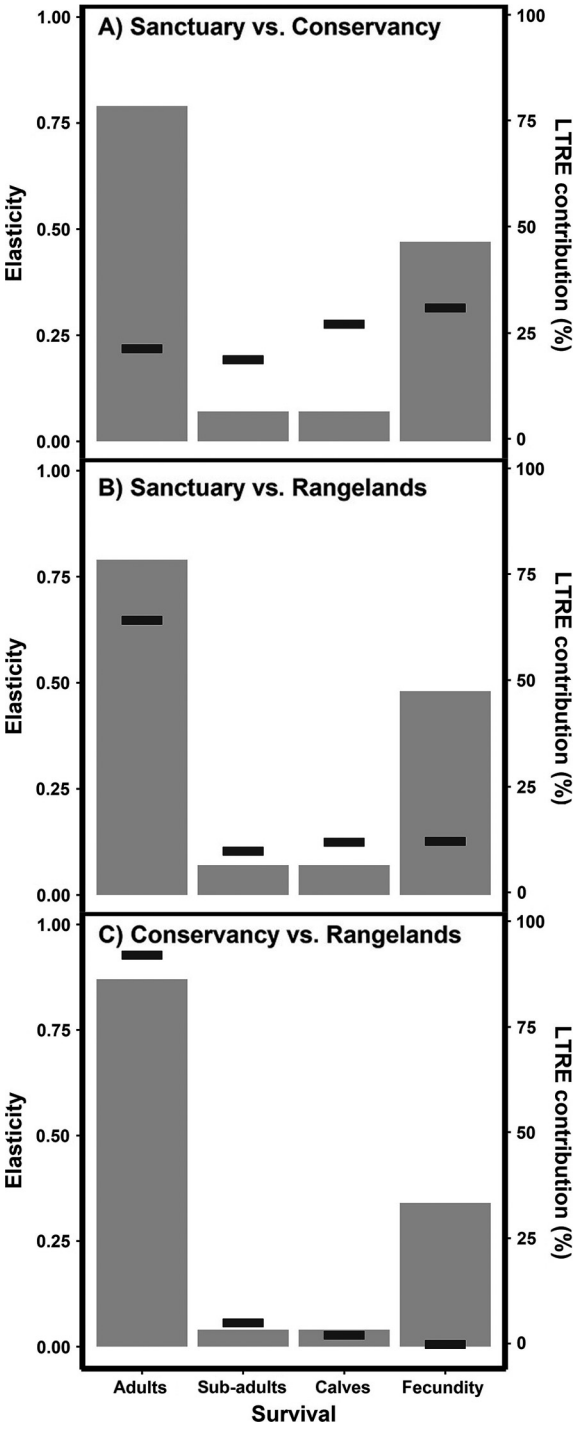

FIG. 3. Results from a life table response experiment (LTRE) indicating the elasticity (bars) and percent contributions (heavy lines) of vital rates for 2012–2015 to changes in λ for hirola for paired settings: (A) sanctuary vs. conservancy, (B) sanctuary vs. rangelands, and (C) conservancy vs. rangelands.

in the sanctuary compared to the rangelands ($Z = 1.71$, $P < 0.01$; Fig. 2E). Fecundity and calf survival were the most important contributors to λ following large carnivore exclusion (Fig. 3A), whereas adult survival was the primary contributor to increased λ stemming from differences in rangeland quality (Fig. 3B, C).

Overall, adult survival contributed most to differences in λ between the conservancy and the rangelands, explaining 90% of the overall change in λ between the two settings (Fig. 3C). Similarly, change in adult survival between the sanctuary and rangelands explained 64% of the overall change in λ between the two settings (Fig. 3B). However, between the sanctuary and conservancy settings, fecundity explained much of the overall change in λ between the two settings (Fig. 3A). For calves, most mortality occurred within the first six months of life, particularly in the conservancy and in the rangelands (Appendix S1: Fig S3).

Discussion

By utilizing a large-scale, large carnivore exclosure and capitalizing on natural variation in rangeland quality, we quantified demographic drivers of the critically endangered hirola antelope in eastern Kenya. Following a rinderpest (*Morbillivirus*) outbreak in 1985 (Andanje 2002), hirola numbers have been suppressed for nearly 30 years (Fig. 1). Although rinderpest was eradicated from Kenya by 2001 (Mariner et al. 2012), hirola populations have never recovered to pre-crash levels, an observation that was the primary motivation for this study. Vital rates for hirola across environmental settings and age classes were suppressed to varying degrees by a combination of predation and rangeland quality, with a decreasing trend in population growth from the sanctuary ($\lambda > 1$) to the conservancy ($\lambda \approx 1$) to the rangelands ($\lambda < 1$). We interpret differences in population growth between the sanctuary and conservancy to reflect the effect of predation by large carnivores, which reduces fecundity and calf survival (Fig. 2A). Population growth between the conservancy and rangelands appears to have shifted from approximately stable to negative, which we attribute to higher rangeland quality in the conservancy.

Some combination of predation and poor range quality was responsible for suppressed population growth of hirola. Population crashes triggered by rinderpest in the mid-1980s have reduced hirola to precariously low numbers, such that their ability to rebound after rinderpest eradication seems compromised by poor habitat quality due to tree encroachment over the past 30 years (Ali et al. 2017). Additionally, and while hirola and large carnivores have coexisted for thousands of years in eastern Kenya, density-dependent predation may prevent positive population growth, confining hirola to a predator pit (Walters et al. 1975, Ballard et al. 2001). In conjunction with efforts to restore grassland habitats, the persistence of hirola likely will also require in situ predator-proof sanctuaries to provide a source for future reintroductions.

Our work strongly suggests that hirola are a refugee species, in which survival and fecundity are not sufficiently high to sustain populations in the remaining habitat (which itself is a fraction of their historical geographic range [Ali et al. 2017]). Overall, the combined effect of increased rangeland quality (stemming from low numbers of livestock) and exclusion of large carnivores resulted in positive population growth of hirola. The reduction in population growth via reduced rangeland quality is consistent with other studies that point to the importance of variation in adult survival in driving population dynamics of tropical ungulates (Owen-Smith and Mason 2005). In contrast, bolstered population growth following predator exclusion fits the life-history paradigm developed in temperate regions, in which calf survival and adult fecundity regulate population dynamics (Gaillard et al. 1998, Raithel et al. 2007). In sum, hirola require some combination of high-quality rangeland and reduced rates of predation, relative to current levels, for populations to persist.

As our study is on a large, critically endangered mammal, our inferences are limited by small sample sizes and at least three potential shortcomings. First, we conducted our work over a relatively short period of time (3 yr) relative to the lifespan of hirola, during which environmental stochasticity (droughts, floods) was minimal and therefore did not feature in our demographic matrices. Second, each environmental setting in our study was represented by a single replicate, in which predator exclusion and livestock production altered the abundance of large carnivores and rangeland quality. Because each setting was not replicated, there is some potential for unmeasured, cryptic effects to influence our results. Finally, some of the demographic pathways by which large carnivores reduced population growth are not known. Although the reduction in adult survival and calf survival show a clear signature of direct killing by predators, it is conceivable that reductions in pregnancy and parturition could have arisen from carnivore-induced stress (e.g., Creel et al. 2009, Sheriff et al. 2015) or behavioral shifts to lower-quality habitats (e.g., Ford et al. 2014, Ford and Goheen 2015, Ng'weno et al. 2017), although the existence and strength of such effects are idiosyncratic and system specific (Kauffman et al. 2010, Middleton et al. 2013).

In African savannas, ungulates exhibit pronounced variation in their abundance through time (Sinclair 1983, Owen-Smith and Mason 2005), and such temporal variation is typically associated with some combination of heterogeneity in rangeland quality and predation (Mduma et al. 1999, Sinclair et al. 2003, Owen-Smith and Mason 2005, Grange et al. 2015). Additionally, our findings are congruent with those indicating that tree encroachment (resulting from elephant extirpation and overgrazing) triggered rangeland degradation and loss of habitat for hirola; tree encroachment was not associated with increased rates of predation (Ali et al. 2017). Since the mid-1980s, hirola have remained at low population densities throughout their geographic range, during which time large-carnivore abundance has remained relatively constant in these areas (Ali et al. 2017). In light of this, and while predation by large carnivores certainly suppresses population growth, we believe rangeland degradation is a major, largely unappreciated threat underlying chronic low numbers of hirola.

The finite rate of population change of hirola was driven by fecundity and calf survival following large carnivore exclusion, whereas adult survival was the primary contributor to increased population growth that stemmed from enhanced rangeland quality. Therefore, and to the extent that large-carnivore control is both unethical and infeasible, the persistence of hirola may depend on the reversion of tree encroached areas to grasslands in eastern Kenya. Our work provides evidence that can be used to integrate hirola conservation and future reintroduction efforts with rangeland restoration. Restoration efforts will require strong local support, and conservation agencies may consider implementing restoration practices that are compatible with local livelihoods. From a parallel study, we found that locals were strongly supportive of manual tree removal, grass seeding, elephant conservation, and resting range from livestock as restoration solutions to promote grass growth and potential recovery of hirola (A. Ali, et al. *unpublished manuscript*). Such efforts hold promise in bolstering hirola populations in landscapes occupied by large carnivores, humans, and their livestock.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1664/full

Data Availability

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.480tf.