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# Savanna herbivore dynamics in a livestock-dominated landscape. II: Ecological, conservation, and management implications of predator restoration

*Nicholas J. Georgiadis*[a,*], *Festus Ihwagi*[b], *J.G. Nasser Olwero*[c], *Stephanie S. Romañach*[d]

[a]*Mpala Research Centre, P.O. Box 555, 10400 Nanyuki, Kenya*
[b]*Save the Elephants, P.O. Box 54667, 00200 Nairobi, Kenya*
[c]*World Wildlife Fund – US, 1250 24th Street, NW, Washington, DC 20037-1193, USA*
[d]*University of Zimbabwe, P.O. Box 167, Mount Pleasant, Harare, Zimbabwe*

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ABSTRACT

Conserving African wildlife in human-occupied landscapes requires management intervention that is guided by a mechanistic understanding of how anthropogenic factors influence large-scale ecological processes. In Laikipia District, a dry savanna region in northern Kenya where wildlife share the landscape with humans and livestock, we examined why five of nine wild ungulate species suffered protracted declines on properties receiving the greatest conservation investment. Of 10 alternative causes examined, only an increase in predation, interacting with brief periods of high and low rainfall, was consistent with the timing, synchrony, duration and species composition of observed ungulate declines.

The principal factor causing predation to increase was a shift in land use from cattle ranching, under which predators and plains zebras were severely suppressed, to wildlife conservation and ecotourism. This prompted a 5-fold increase in plains zebra abundance, and created a demand for living predators. Plains zebras ultimately comprised more than half the available prey biomass, and supported a substantial predator community, but were not limited by predators. We infer that increasing predation pressure caused predator-susceptible prey species to decline, via mechanisms that included apparent competition.

Herbivore dynamics in Laikipia shared features with previously reported responses by prey communities to predator manipulation in Kruger and Serengeti National Parks. All featured one or a few numerically dominant herbivore species, which were primarily limited by rainfall and density, supporting a predator community that in turn limited the abundance of other prey species. In each case, predation had a profound effect, but on only a subset of prey species, reducing the evenness component of prey diversity.

The presence of cattle in the landscape may affect predator–prey dynamics in both direct and indirect ways, depending on rainfall. In extreme years (floods or drought), episodic die-offs temporarily subsidize scavenging predators. In low rainfall years, competition between plains zebras and cattle, which negligibly support predators, may indirectly limit predator carrying capacity. Consequently, removal of cattle may favor not only zebras, but also their predators, and further depress predator-susceptible prey species.



* *Corresponding author*: Tel.: +254 62 32752; fax: +254 62 32750.
E-mail address: njg@mpala.org (N.J. Georgiadis).
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## 1. Introduction

The persistence of wildlife in African drylands will depend more on its viability in non-protected areas than in national parks and reserves (Western, 1989; Hutton et al., 2005). This is because the ecological processes that ensure survival of large mammal populations in drylands, such as seasonal migration by elephants (*Loxodonta africana*), typically extend far beyond the relatively small sections that are formally protected within larger landscapes. To a greater degree than pertains in most protected areas, where little or no management intervention is the norm, conservation in non-protected landscapes entails active management of wildlife towards stated conservation goals. This in turn depends on a mechanistic understanding of wildlife dynamics, their interactions with livestock, and how anthropogenic factors influence large-scale ecological processes.

Laikipia District is a non-protected savanna region in northern Kenya where abundances of wild and domestic ungulates vary inversely with each other among three principal land-use types (Georgiadis et al., 2007): 'group ranches' that are communally-owned by a limited number of families, mainly practicing pastoralism, large-scale commercial ranches where cattle are managed at moderate to low densities and wildlife are favored ('pro-wildlife' properties), and the remainder ('transitional' properties), on which wildlife is tolerated at best, or actively discouraged. Intensive conservation activities in this region, aimed at maintaining integrity of ecosystem processes across a mosaic of properties with contrasting land uses, have provided instructive case studies for large mammal conservation in human-occupied landscapes (Georgiadis et al., 2003, 2007; Woodroffe and Frank, 2005).

Modeling of ungulate population time series showed the abundance of dominant herbivores in this system to vary greatly with land use type, and to be limited by rainfall (cattle and plains zebra *Equus burchelli*), or regulated by factors related to density (plains zebra and giraffe *Giraffa camelopardalis*; Georgiadis et al., 2003, 2007). Five other wild herbivore species were shown to have declined steadily over at least a decade (waterbuck *Kobus ellipsiprymnus*, Thomson's gazelle *Gazella thomsoni*, buffalo *Syncerus caffer*, eland *Taurotragus oryx*, and hartebeest *Alcelaphus buselaphus*). Declines on pro-wildlife properties were particularly severe, amounting to 37% of total wild herbivore biomass (excluding elephants) between 1990 and 2005. Since these properties received the highest conservation investment, with many relying on income from ecotourism, herbivore declines were neither intended nor understood. At face value, their magnitude questioned whether even substantial investment is sufficient to conserve wildlife in non-protected areas. We examined and attempted to interpret the observed population declines.

On 'transitional' properties in the west, south, and southeast of Laikipia District, human-related factors associated with land subdivision and land use change, such as expanding habitation and cultivation, bushmeat hunting, and dramatic increases in sheep and goat densities, have contributed to wildlife declines over recent decades (Georgiadis et al., 2007). On drier group ranches in the north-east, persistently high livestock densities displaced much of the wildlife long before the first District-wide ungulate census in 1985. However, increasing habitation, cultivation, and livestock cannot directly account for wild herbivore declines on pro-wildlife ranches, where habitation and cultivation have remained negligible, and livestock densities have not increased for decades (Georgiadis et al., 2007). Of additional interest was why other wild species did not decline on pro-wildlife properties (plains zebra, Grant's gazelle *Gazella grantii*, impala *Aepyceros melampus*, and giraffe).

Seeking to understand the causes of observed declines, hartebeest was selected for closer scrutiny for four reasons. This species appeared to be the most sensitive indicator, declining by a greater proportion than any other (78% since 1991). Second, this is a sedentary species, living in groups with relatively small home ranges. Individuals on pro-wildlife properties were therefore less likely to be directly affected by factors causing declines on other land-use types. Third, nematode lungworm parasites were implicated as a factor contributing to its decline, and we explicitly addressed this possibility. Finally, the population in Laikipia District is the largest of only three distinct populations of *A. buselaphus* remaining in Kenya that are hybrid between two morphotypes (*A. b. cokei* and *A. b. lelwel*), the remainder having been extirpated by human population growth, habitat loss and land use changes. Hartebeest is therefore a flagship species for Laikipia, and will require informed management intervention to secure its survival.

Focusing on hartebeest as a special case, but generalizing to other species where appropriate, we examined seven additional factors to the three discounted above (displacement by habitation, cultivation and livestock) that might have caused ungulate declines on pro-wildlife properties. For these factors, available data permitted a direct test, or qualitative information permitted a reasoned evaluation. The first two are human-induced: over-consumption, either due to bushmeat hunting or sanctioned harvesting. The remaining five are ostensibly 'natural': exceptional rainfall patterns, inter- and intra-specific competition, parasitism, and predation.

## 2. Methods

The study area, sample survey methods, and the histories of rainfall, land use, and wildlife harvesting have been described in Georgiadis et al. (2003, 2007).

### 2.1. Lungworm sampling

Hartebeest fecal pellets sampled to assess lungworm prevalence were cooled and processed within 48 h of collection. The Baermann technique (Bowman, 1999) was used to concentrate and recover lungworm larvae, which were stained with iodine. Lungworms mostly of the genera *Protostrongylus* spp., but also *Muellerius* spp., and *Dictyocaulus* spp., were distinguished under dissecting microscope using descriptions by Bowman (1999). Hartebeest density was estimated using minimum convex polygons defined by the geographic extents of cumulative hartebeest distributions on each property, with the position of each herd recorded with a Garmin *GPSmap76S*. Hartebeest were counted, aged as to calf (0–6 months), subadult (6–24 months) and adult (>24 months), and sexed by