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

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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.

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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 eco-tourism, 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 south-east 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), sub-adult (6–24 months) and adult (>24 months), and sexed by

two observers during census loops driven monthly on each property. Data for lungworm prevalence and hartebeest population age structure were root arcsine-transformed for ANOVA, with which variation was sought over time, with host density, and among ranches.

3. Assessment of potential causes of ungulate decline

Each of seven possible causes of population decline on pro-wildlife ranches were assessed in turn.

3.1. Bushmeat hunting

Data are lacking to test directly whether consumption of wildlife caused the observed declines, but this is largely because, exceptionally, bushmeat hunting is not prevalent on pro-wildlife ranches in Laikipia District. Each has its own security system, and most are functionally well-protected. Long aware of declines in selected ungulate species, and of the possibility that bushmeat consumption was a leading cause, ranch managers consistently asserted that incidents of bushmeat consumption were far from frequent or severe enough to have caused declines of the magnitude and duration observed (personal communication). Additional observations are consistent with this assertion. For example, losses to snares of livestock and radio-collared predators are rare. Impala, a favored bush-meat species, declined on transitional properties, but did not decline on pro-wildlife properties (Georgiadis et al., 2007). By contrast, waterbuck are not preferred by bushmeat hunters, yet their numbers declined precipitously on pro-wildlife ranches. Eland are favored by bushmeat hunters,

and of the declining species is the only one to move between pro-wildlife and transitional properties. Therefore, bushmeat hunting may have contributed to the decline of eland when they move off pro-wildlife ranches, but is unlikely to have directly affected other species to an extent that could account for the observed declines.

3.2. Legal harvesting

In 1992, harvesting of wild ungulates resumed in Laikipia District after a hiatus of 15 years, involving 8 of the most abundant species (plains zebra, Grant's and Thomson's gazelles, impala, buffalo, eland, waterbuck, and giraffe). Harvesting continued until 2003 when it was again suspended nationwide. Quotas were initially set at 15% of the censused population size, but were later reduced (Georgiadis et al., 2003). Harvest records, available from 1997 onwards, show that quotas for each species in 1997 and 1998 varied between 6% and 11%, but declined thereafter to mostly 6% (Table 1). Several observations suggest that over-harvesting played little role in the declines of wild herbivores in Laikipia. First, of the species that declined, hartebeest were never harvested, and numbers of waterbuck taken in any year were negligible (Table 1). Second, quotas were never filled for any species. The maximum proportion actually harvested for any species after 1997 was 5%, for plains zebra, a species that did not decline (Georgiadis et al., 2003). For other species, harvests amounted to less than 3% of the population per year, and most individuals taken were adult males. In the absence of other factors, such low harvesting rates are unlikely to have caused such marked declines, even in larger-sized, more slowly reproducing species.

Table 1 – Ungulate population estimates, harvesting quotas, and actual harvests in Laikipia District, 1997–2003

Species		1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003
Buffalo	Population	2655	1937	2717	2524	1666	1550
	Quota (%)	8	10	3	6	6	6
	Harvest (%)	1	–	2	1	2	2
Eland	Population	3667	5329	2933	2725	2417	1450
	Quota (%)	6	10	6	6	6	6
	Harvest (%)	1	–	1	0	1	1
Giraffe	Population	1856	1498	1543	1433	1720	1597
	Quota (%)	5	10	6	–	–	–
	Harvest (%)	4	–	2	–	–	–
Grant's Gazelle	Population	6997	7602	5254	4881	9072	4000
	Quota (%)	0	10	8	6	3	6
	Harvest (%)	0	–	0	1	1	2
Impala	Population	8436	8748	5714	5309	4391	4667
	Quota (%)	8	10	8	6	7	6
	Harvest (%)	3	–	3	2	3	4
Plains Zebra	Population	35859	31797	32725	30405	26095	29114
	Quota (%)	11	10	6	6	6	5
	Harvest (%)	5	–	5	3	5	4
Thomson's Gazelle	Population	5150	5846	4035	3749	4038	3450
	Quota (%)	5	10	6	6	5	6
	Harvest (%)	3	–	3	2	3	3
Waterbuck	Population	621	688	279	259	389	183
	Quota (%)	8	10	6	6	3	6
	Harvest (%)	1	–	0	2	0	0

The harvesting year was from March 1 to February 28. Harvest figures were not available for 1998–1999 (source: Laikipia Wildlife Forum).

3.3. Rainfall-dependence

Forty-year series of daily rainfall data from five gauging stations scattered across the pro-wildlife ranches of Laikipia District were used to test whether changing rainfall patterns could account for observed herbivore declines (Fig. 2 in Georgiadis et al., 2007). There was no tendency for mean annual rainfall to decline over the 40 years between 1965 and 2005, or between 1997 and 2005 ($P > 0.05$), the period of greatest ungulate decline (Georgiadis et al., 2007). Indeed annual rainfall was higher than the 40-year mean for 6 of those 9 years. Similarly, mean dry season rainfall showed no overall trend, or marked decline between 1997 and 2005 (Fig. 1; however, there was a prolonged period of low dry season rainfall between 1970 and 1976, and a marked decline in dry season rainfall between 1978 and 1987).

Previous analyses showed that cumulative departure from mean monthly rainfall (referred to as the Rainfall Deficit Index by Georgiadis et al., 2007) influenced the dynamics of hartebeest, Thomson's gazelle, and giraffe from 1985 to 1997, when their numbers were relatively high (depicted for hartebeest in Fig. 2). Thereafter, the rainfall signal in ungulate time series declined, and was not significant in the dynamics of any of the species on pro-wildlife properties (Georgiadis et al., 2007). Results of the June 1997 sample survey marked the first time in the series that hartebeest numbers failed to increase when rainfall increased. Projection beyond 1997 of the purely rainfall-dependent model fit to hartebeest numbers prior to February 1997 provided an expectation that their numbers should have increased initially, then declined, then increased again when the region experienced the a 5-year run of above average rainfall (2001–2005). Instead the population declined exponentially throughout this period (Fig. 2).

The apparent transition in dynamics from dependence on rainfall to hitherto unidentified factors coincided with the beginning of an exceptionally wet El Niño event, which was immediately followed by an exceptionally dry La Niña event, each lasting about two years (1997–2001). These were, respectively, the wettest and driest two-year periods in 40 years of rainfall records, and amounted to a severe perturbation to the ecosystem. During the wet phase, unknown numbers of livestock (mostly small stock) succumbed to

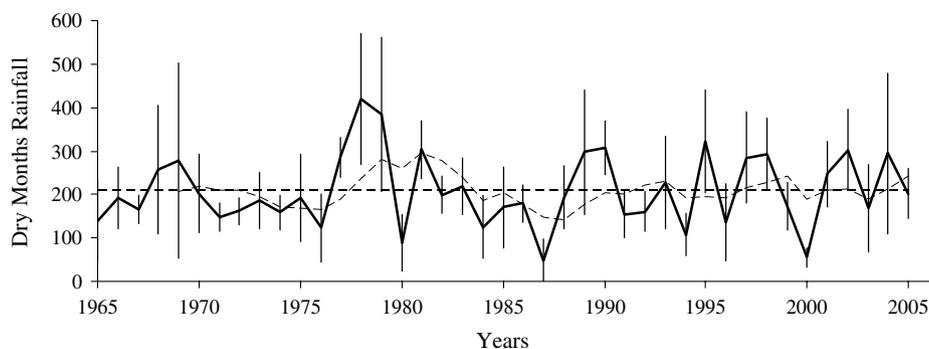


Fig. 1 – Mean dry season rainfall (sum of rain falling in the six driest months: January, February, March, September, October and December) over 40 years from five gauging stations scattered across the study area (bold black line, with standard deviations). The 5-year moving average (dotted line) and long-term mean (208.5 mm; dashed line) are also given.

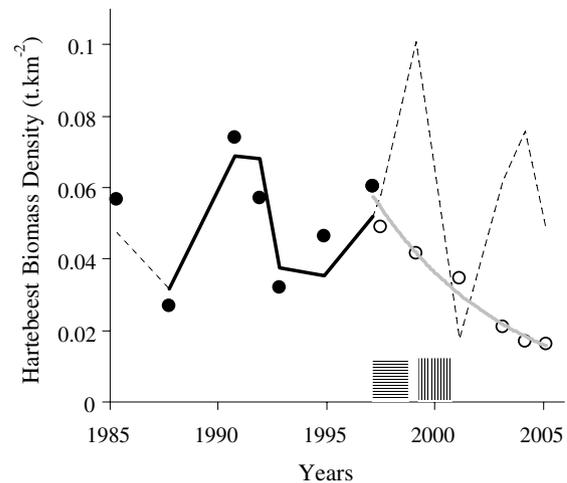


Fig. 2 – Changes in hartebeest population density on pro-wildlife properties in Laikipia District, 1985–2005 (circles), divided into an initial phase (1985–1997; filled circles) during which the population was rainfall-limited, and a latter phase when the population declined steadily (1997–2005; open circles). The initial phase was modeled by $\ln(y) = 0.097x - 3.051$ ($r = 0.87$, $n = 6$, $P < 0.05$; solid black line), where x is the Rainfall Deficit Index from one census to the next. The rainfall-limited model is projected beyond 1997 (dotted black line) to show how the observed population trajectory deviated radically from expectations based solely on rainfall. The exponentially declining phase was modeled by $y = 9E + 139e^{-0.16x}$, where x is Year ($r = 0.99$, $n = 7$, $P < 0.001$; solid grey line). The timing of the El Niño floods and La Niña drought is indicated along the x-axis by horizontal and vertical hatching, respectively.

mosquito-born viral diseases like Bluetongue and Rift Valley Fever. It is possible that wild ruminants were also affected, but this was not recorded, even on properties where small stock died in large numbers. By the end of the dry phase two years later (March, 2001), numerous domestic and wild herbivores had succumbed to drought, particularly cattle, plains zebra, and buffalo. These extreme climatic events therefore had negative effects on livestock during both wet

and dry phases. Vital rates of wild herbivores certainly declined during the drought (see Georgiadis et al., 2003 for zebras), and possibly also declined during the wet phase due to disease.

Disease and drought associated with exceptional rainfall patterns of 1997–2001 may therefore have contributed to observed declines in hartebeest and other wild ungulates. However, failure of these species to increase following the drought, when annual rainfall was above-average (but neither excessive, nor aseasonal) for 5 years, suggests either that the effects of drought and disease somehow persisted long after 2001, or, more likely, that disease and drought were not the sole causes of decline.

3.4. Intra-specific competition

Density-dependence was detected in the time series of only two species, plains zebra and giraffe (Georgiadis et al., 2003, 2007), but this is not a factor likely to cause protracted declines on its own. In fact, giraffe declined only initially on pro-wildlife properties, and plains zebras recovered after the drought-induced decline in 2000–2001. It is conceivable that factors related to density played an undetected regulatory role in the dynamics of other species, including those that subsequently declined. But if so, a compensatory effect causing populations to increase at low density would have been expected following the severe drought that ended in March 2001, when rainfall was above-average for 5 years. No such response was observed.

3.5. Inter-specific competition

Declines may have been caused by competitive interactions among a subset of wild herbivore species. For instance, a 5-fold increase in plains zebra numbers (Georgiadis et al., 2007; and below) may have negatively influenced other grazing species (hartebeest, buffalo, and waterbuck). This is unlikely because plains zebra numbers did not increase persistently beyond 1992, yet declines in buffalo, hartebeest and waterbuck numbers were not persistent until after 1997. Nonetheless, lagged effects on other grazers due to the increase in plains zebras, perhaps via to vegetation changes, cannot be excluded.

It is also conceivable that increasing sheep and goat densities on transitional properties indirectly caused wild herbivore declines on pro-wildlife properties, for example, by compressing zebras into pro-wildlife properties. Yet there was no association between zebra density on pro-wildlife properties and sheep and goat density, or total livestock density, on transitional properties, either concurrently, or from preceding censuses ($r < 0.25$, $n = 12$, $P > 0.46$). Most compelling, for plains zebras to continue to compete with other wild grazing species when the combined biomass of the latter had declined by 67% at the end of the drought in 2001, after which rainfall was above-average for 5 years, would invoke a compounding effect of competition during an exceptionally prolonged period of non-limiting rainfall. We infer that competition for food was unlikely to have contributed to protracted declines among wild herbivore species on pro-wildlife properties.

3.6. Parasitism in hartebeest

The possibility that nematode lungworm parasites compromised the viability of hartebeest in Laikipia District was raised during the drought in 1999–2001. On three separate occasions on northern ranches individual hartebeest were found recently dead from no obvious cause (they had not been killed by predators, and were not overly emaciated). All had severe lungworm infestations.

To examine the potential impact of this parasite, the prevalence of lungworm, as well as host age structure, were monitored monthly between March 2004 and March 2005 on four contiguous properties at the core of the hartebeest range (Mpa-la, Segera, Ngorare, and El Karama ranches; Fig. 3). In October 2004 and March 2005 similar data were recorded on Solio ranch in the south of Laikipia District, where hartebeest densities were greater than elsewhere by factors of 2–4. There was no trend in lungworm prevalence over the 12-month monitoring period ($F = 0.18$, $df = 1, 33$, $p = 0.67$), and a non-significant tendency for prevalence to increase with host density ($F = 1.93$, $df = 1, 33$, $P = 0.17$; Fig. 4). However, differences in lungworm prevalence among ranches were highly significant ($F = 11.46$, $df = 4, 33$, $p < 0.001$), as were differences in host age structure ($F > 5.51$, $df = 4, 50$, $P < 0.001$), particularly between the four core ranches and Solio ranch (Fig. 5). Segera had relatively fewer calves than elsewhere, and Solio had relatively more sub-adults and fewer adult females than elsewhere (Fig. 5).

Since lungworm prevalence was highest on Solio ranch, where hartebeest densities and proportions of calves and sub-adults were also highest, it did not appear that lungworms were adversely affecting host birth and survival rates, at least on that property in 2004–2005. It remains possible that survival of adult hartebeest in Laikipia was compromised by lungworm during the drought of 1999–2001. Over the following 5 years, however, rainfall was above-average, yet the (overall) Laikipia hartebeest population continued to decline. We infer that, if lungworm adversely affected hartebeest viability in Laikipia, this was more likely to be during the severe drought of 1999–2001, and was not the only factor causing the protracted population decline. Moreover, because *Protostrongylus* spp. is largely specific to Alcelaphines (Grootenhuis, 1999), lungworm was unlikely to have been a factor in the declines of other species. A separate study that monitored strongyloid parasites in wild ruminants in Laikipia found elevated fecal egg counts during drier periods in six out of nine species (Ezenwa, 2004). These included species that declined (hartebeest, waterbuck, eland, Thomson's gazelle), as well as those that did not decline (impala, Grant's gazelle), and may simply result from ingesta throughput rates declining faster than parasite egg production rates with declining food quality.

3.7. Predation

Lack of data showing how predator numbers and preferences for prey have changed over recent decades precluded a numerical test of the hypothesis that wild herbivore declines in Laikipia District were caused by increasing predator numbers. It is unlikely that predation would cause such protracted declines in prey abundance under 'natural' conditions, but

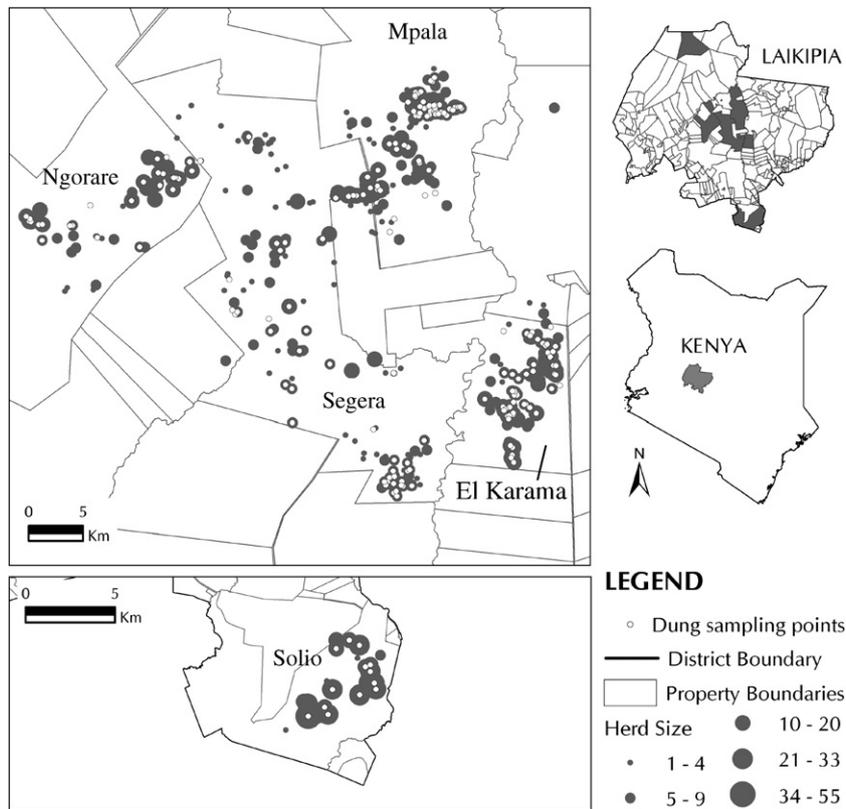


Fig. 3 – Cumulative distribution of hartebeest (grey circles) on five ranches in Laikipia District (insets) in 2004–2005 that were detected in monthly censuses. Also shown are locations at which dung was sampled for parasite analysis (small white circles). Mugie is the northern shaded ranch in the inset of Laikipia.

profound changes in management of both predators and prey over recent decades (Romañach et al., in press) caused predator–prey dynamics to be far from natural. We review evidence that predation played a role in the observed herbivore declines.

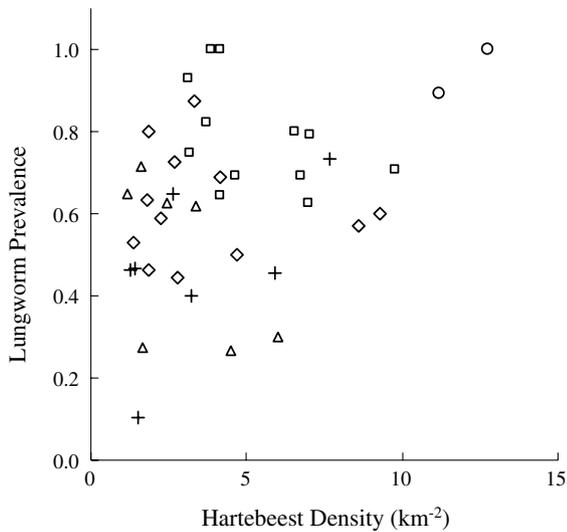


Fig. 4 – Variation of monthly lungworm prevalence with hartebeest density on four core ranches in Laikipia: Segera (pluses), Mpala (diamonds), Ngorare (triangles), El Karama (squares), and on Solio (circles).

Restoration of predators in Laikipia District: Until the early 1990s livestock ranching was the predominant land use on what are referred to here as pro-wildlife properties in Laikipia District. A survey of management practices and the status of wild ungulates in the late 1960s reported that consumptive use of wildlife, including commercial sport hunting, sale of skins and trophies, and shooting for meat, supplemented income and protein on all but two of 42 large-scale ranches (Denney, 1972). The main predators present in Laikipia at the time

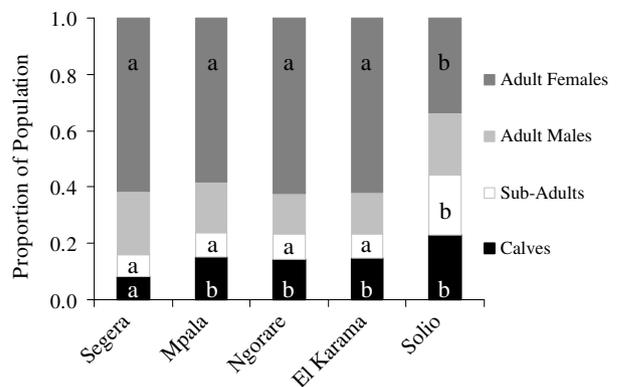


Fig. 5 – Mean age structure of hartebeest on four core ranches and Solio ranch in Laikipia District between 2004 and 2005 (letters denote significance according to Tukey’s paired contrasts, $\alpha = 0.05$).

of Denney's survey (and the proportion of ranches reporting livestock losses to them) were hyena (45%), lion (31%), leopard, (31%), wild dog (12%), cheetah (10%), and jackal (10%). Denney (1972) reported that livestock losses from predation were reduced "by shooting [predators], the use of gin (steel) traps and live-traps, poison baits and, to some extent, herding practices. . . The majority of ranchers used carcasses or kills poisoned with strychnine or toxaphene. Dogs [were] used extensively by some ranchers to flush, trail, and 'tree' or bag predators such as lion, leopard, cheetah, hyena, and sometimes jackal". At that time, livestock losses were reduced more by stringent predator suppression than by herding practices.

The herding practices that prevailed at that time relied largely on livestock fences, not only around property perimeters but also dividing properties into large paddocks (only three ranches had none of their perimeter fenced; 33 of 42 ranches had interior fencing, with a mean of 32 paddocks per ranch; Denney, 1972). On the more 'developed' ranches (25 of the 42 properties), predators were rare enough for cattle to be grazed out in paddocks overnight. Paddock fencing was progressively removed from most properties from the late 1970s, largely due to escalating damage caused by a growing elephant population (Littlewood, personal communication). Today, conditions are radically changed: few properties have perimeter fences, and most of those that exist are designed to manage wildlife, not livestock. As fences were removed, the management practice of herding cattle at night into predator-resistant enclosures ('bomas') increased, and is currently the method used to minimize livestock losses to predation on all of the pro-wildlife properties. Suppression of all predator species eased as herding practices changed, but continued on some properties through the 1990s (Woodroffe and Frank, 2005; Woodroffe et al., 2005; Frank et al., 2005).

Plains zebras were also considered detrimental to ranching, due to perceived competition with cattle, and were also heavily suppressed (Denney, 1972, and personal communication with long-term residents of Laikipia District). In the late 1960s, the sum of subjective estimates given by ranchers of plains zebra numbers on their land was only 6210 (Denney, 1972). Yet 90% of ranchers interviewed by Denney expressed tolerance for other wild ungulate species that were not considered directly detrimental to ranching. Indeed ranchers' estimates of numbers of 'tolerated' species were similar to or greater than estimates from the first sample survey of Laikipia District in 1985 (Georgiadis et al., 2007). By that time, suppression of plains zebras had eased, partly because of a national ban on wildlife consumption in 1977, and zebra numbers had increased to over 20 000. By September 1990 plains zebra numbers had further increased to over 30 000, and were approaching their rainfall-dependent carrying capacity (Georgiadis et al., 2003). Wild herbivore biomass density on pro-wildlife properties in 1990 (2.55 t km^{-2} , Fig. 3 in Georgiadis et al., 2007) was higher than has been recorded in any sample survey before or since. Given that the ban on wildlife consumption in 1977 did not prohibit predator removal intended to protect livestock, we infer that predator suppression was a primary contributor to the high wild herbivore abundance in 1990.

Such high wild herbivore abundance motivated landholders to lobby for the resumption of sanctioned harvesting. As

described above, harvesting resumed in 1992, and the Laikipia Wildlife Forum was created to coordinate its management (LWF is a formally registered association of landholders with a shared interest in wildlife conservation). Soon thereafter, an enthusiastic conservation movement gained momentum in the region, and a rapidly growing number of LWF members ventured into ecotourism (today more than 30 tourism enterprises depend on the wildlife resources in Laikipia; see www.laikipia.org). This created a demand for living predators of all species on ranches with an interest in tourism and conservation, and prompted a reduction in predator suppression. Therefore, reversals in attitude and management practices caused plains zebras to increase in Laikipia District by a factor of about five between the late 1960s and 1990, and a gradual easing of predator suppression through the 1990s. As a result, predators are more abundant in Laikipia today than 15 years ago, and far more abundant than 30 years ago (Romañach et al., in press). Compared to results of the survey by Denney (1972) in the late 1960s (reported above), proportions of commercial ranches reporting livestock losses in 2004 had increased greatly for lions (+65%) and leopards (+30%), but losses to hyena (+3%), wild dog (−8%), cheetah (+7%), and jackal (−4%) were little changed (Romañach et al., in press). Increased tolerance of predators was also reflected in the re-colonization of Laikipia by wild dogs in 2000.

The predation hypothesis entails that declining prey species (hartebeest, eland, waterbuck, buffalo, and Thomson's gazelle) were more susceptible to or preferred by predators than are species that declined mildly or not at all (plains zebra, Grant's gazelle, impala, giraffe). At least for plains zebras and hartebeest, available evidence supports this assertion. By the late 1990s, and we assume long before, large predators were consuming more plains zebras than any other prey species (Frank, 1998), simply because zebras comprised more than half the available prey biomass (Georgiadis et al., 2007). Yet modeling has shown that zebras continue to be limited by rainfall and factors related to density, not predation (Georgiadis et al., 2003, 2007).

By contrast, three observations support the notion that hartebeest are susceptible to predation. First, increased mortality among younger age classes is consistent with the comparative scarcity of calves and sub-adults on Mpala, El Karama, Ngorare and Segerera ranches, where predators are abundant, compared to Solio ranch (Fig. 5), from which large predators have been absent for decades.

Second, a better-controlled 'predator removal' comparison was afforded in February 2003 when the home range of an existing group of five hartebeest was enclosed within a predator-proof reserve established for captive white rhinos (*Ceratotherium simum*) on Mugie Ranch in northern Laikipia. The group comprised an adult male, three adult females, and a sub-adult male, the scarcity of calves reflecting the age structure on the four core ranches recorded a year later (Fig. 5). Over the following 24 months, five calves were born and all individuals survived to at least July 2005 (Mortensen, personal communication). When protected from predators, therefore, hartebeest numbers within the Mugie sanctuary doubled in two years. Neither instance was entirely free of confounding factors, since the hartebeest on both Solio and Mugie ranches had access to mineral licks provisioned for livestock and rhi-

nos, respectively. Nonetheless, these observations are consistent with the notion that predation was a significant factor in the dynamics of hartebeest in Laikipia, and by implication other species, at least latterly.

Third, hartebeest have become effectively extinct within two fenced wildlife reserves in the region, apparently due to predation by lions. In one instance, 150 hartebeest were translocated into the Solio Reserve (which is separated from Solio Ranch by a predator-proof game fence) in the mid-1970s. All but two had been killed within a few years (E. Parfet, personal communication). Similarly, on Lewa Wildlife Conservancy (LWC), a fenced reserve that adjoins Laikipia District to the east, hartebeest numbers declined steadily from 58 to 1 in 8 years following re-colonization by lions in 1997 (unpublished data, LWC). Although hartebeest were predator-naïve in both cases, so were other prey species at LWC. Waterbuck, eland, Grevy's zebra (*Equus grevyi*) and oryx (*Oryx gazella*) also declined at LWC, but not as steeply as hartebeest. Plains zebra and giraffe numbers were intentionally reduced by translocation (to reduce potential competition with Grevy's zebra and black rhino, *Diceros bicornis*, respectively). Buffalo showed no overall trend, and impala and Grant's gazelle numbers increased. With the exception that buffalo did not decline on LWC, apparent susceptibility to predation was similar among species occurring in both Laikipia District and LWC.

A climatic perturbation Floods and drought associated with extreme El Niño and La Niña events between 1997 and 2001 (described above) contributed to a reduction in the biomass of cattle and wild herbivores in Laikipia District of approximately 24%. Vegetation cover increased dramatically during an exceptionally long growing season from March 1997 to December 1998 (an above-average growing season lasts 3 months). This probably favored stalking predators (Mills et al., 1995), and improved predation success, at least temporarily. Monitoring of vegetation biomass and composition on large-scale plots (Young et al., 1998) throughout this period showed that changes brought about by the El Niño rains in 1997–1998, manifested as high grass biomass and a proliferation small woody species, were reversed by the ensuing drought (Young, personal communication). During the drought, large numbers of wild herbivores succumbed to starvation, as did pastoralist livestock, while their owners sought grazing across the District. During four years of disease and starvation, therefore, dead and dying herbivores, both wild and domestic, were abundantly available to predators. A possible consequence of these exceptional climatic conditions was that predators increased in Laikipia, at least temporarily.

4. Discussion

Of 10 factors potentially contributing to observed ungulate declines on pro-wildlife ranches in Laikipia District, the following could not be ruled out: bushmeat hunting of eland when they moved off pro-wildlife properties; short-term effects of disease associated with an exceptionally wet El Niño event in 1997–1998; short-term effects of drought associated with an exceptionally dry La Niña event in 1999–2001, possibly interacting with lungworm in hartebeest; strongly lagged effects on other grazing species due to increasing plains zebra

numbers; and the restoration of predators. All may have contributed, additional unidentified factors cannot be ruled out, and causality between predator restoration and ungulate declines was only implicit. Nonetheless, that predators were restored is well established, and this was unlikely to have had undetectable effects on prey populations. Moreover, predator restoration was the only factor that, by itself, could explain not only declines among multiple prey species with contrasting food and habitat preferences, but also the synchrony, long duration, and lagged timing of declines, relative to the shift in land use from ranching to conservation and ecotourism that began on pro-wildlife ranches in the early 1990s. Accordingly, we focus the discussion on ecological, conservation and management implications of predator restoration.

Three additional factors may have influenced herbivore declines, but could not be directly assessed. First, long-term residents assert that woody vegetation cover has increased on pro-wildlife ranches after more than 50 years of fire suppression. While herbivore species preferring open grassland may have been adversely affected by loss of habitat over the long term (e.g. hartebeest and Thomson's gazelle, but not buffalo, eland and waterbuck), woody cover has not increased fast enough over the last 15 years to account for the magnitude or steepness of observed declines. In fact, woody cover has recently declined in some areas due to increasing elephant densities (Augustine and McNaughton, 2004; Pringle et al., 2007).

A second factor that may have influenced herbivore declines is micro-nutrient deficiency. Many ranchers in Laikipia supplement their livestock with minerals, which in places have been shown to be deficient (unpublished report on forage analysis for Laikipia by BASF Group, Derbyshire, UK). Even if nutrient deficiencies also limit wild herbivore performance (Sinclair, 1974; McNaughton and Georgiadis, 1986; Augustine et al., 2003), they are unlikely to trigger protracted and selective herbivore declines in the absence of other factors.

Third, undetected pathogens may have compromised the viability of the declining species. Any of these factors would have increased the sensitivity to predation of affected prey species when predator numbers increased, yet predation would remain the only factor appearing to cause declines. Predation may therefore have only proximally contributed to ungulate declines.

Two corollaries of the predation hypothesis are instructive about predator–prey dynamics in Laikipia District, and in general. First, predator suppression prior to the early 1990s was effective, allowing some prey species to attain higher densities than if predators had not been suppressed, approaching limits set by rainfall (Georgiadis et al., 2007). Since the early 1990s, declining prey species have been settling to levels defined largely by predation. Stabilization of declining species is an expected result of prey switching by predators (Mills et al., 1995), but continuing declines suggested the system had not stabilized by February 2005 (Georgiadis et al., 2007). Continued suppression of predators on some properties may have slowed prey declines, but we further note that prey declines can persist under constant predator density (Owen-Smith and Ogutu, 2003).

A second corollary of the predation hypothesis is that the principal factor limiting hartebeest numbers switched from

rainfall ('bottom-up' control) to predation ('top-down' control) in early 1997. This is because the population would not have responded positively to rainfall prior to 1997 if vital rates had been as low as they were after that time. The transition from bottom-up to top-down control appears rapid in hartebeest (Fig. 2), and its coincidence with the onset of the El Niño floods in 1997 suggests that exceptionally high rainfall played a catalytic or interactive role in their decline. However, the transition from bottom-up to top-down control appeared less abrupt for other declining species (Fig. 3 in Georgiadis et al., 2007). It is likely that recovering predator populations began to affect prey well before 1997, while prey populations were high enough also to be limited by rainfall.

An assessment of the separate effects of individual predator species on the prey community in Laikipia is precluded by lack of data on prey preferences. Lions, hyenas, and leopards all increased in abundance, and they are likely to have been the principal agents of increased predation pressure. Cheetahs can be discounted as having had a major impact upon prey because they have always been rare. Wild dogs had little impact because they did not return to Laikipia until 2000, which was long after prey declines had begun, did not achieve similar densities to protected populations for a further 5 years, and largely ranged across group ranches (Woodroffe et al., 2005 and personal communication).

Comparison of observations in Laikipia with instances of predator manipulation in other savanna systems provides insights into how predation might shape savanna prey communities. Similarly protracted, but even greater declines among a sub-set of prey species in Kruger National Park began in the mid 1980s. In that case, declines were ascribed to a prolonged period of low rainfall, and associated vegetation changes (Owen-Smith and Ogutu, 2003; Ogutu and Owen-Smith, 2003; Dunham et al., 2004), as well as to increasing predation, due indirectly to the installation of wells in drier areas (Harrington et al., 1999; Owen-Smith and Mason, 2005; Owen-Smith and Mills, 2006). Provision of drinking water induced numerical responses among the more water-dependent prey species (primarily plains zebra), which in turn caused local predator densities to increase.

Among prey species common to the studies in Kruger NP and Laikipia, those that declined steeply (eland, waterbuck and buffalo), and those that declined mildly or not at all (plains zebra, giraffe and impala) were the same in both systems. Although anthrax contributed to declines of buffalo in Kruger (Owen-Smith and Ogutu, 2003), correspondence between the two systems in the identities of declining and stabilizing species is striking. It implies either that structural habitat similarities between Laikipia and Kruger NP influenced predator-prey interactions in homologous ways, or that elements of susceptibility to predation are intrinsic to prey species, or both.

Body size was (inversely) associated with susceptibility to predation by non-migratory prey in northern Serengeti National Park, where smaller-bodied prey species (including impala) increased dramatically upon temporary reduction of predators in the 1980s (Sinclair et al., 2003). Prey body size did not correlate significantly with predator preferences in Kruger NP ($r = -0.32$, $n = 8$, $P > 0.05$; data from Harrington et al., 1999), or with rate of prey species decline in Laikipia

($r = -0.39$, $n = 9$, $P > 0.05$; data from Georgiadis et al., 2007), although trends were in the expected (negative) direction in both cases. Declining species in Laikipia tended to be those that occurred in small groups, or more wooded habitats, or both, implying concealment and detection of both predators and prey were important factors (Hopcraft et al., 2005).

Prey responses to predator addition or removal in Kruger NP, Serengeti NP, and Laikipia District were also consistent in that the magnitude of predator effects on prey populations did not become apparent until these systems were perturbed. At that point, predation was seen to profoundly affect the structure of these prey communities, reducing the abundance of some species, but having little apparent effect on others. In all cases, predation reduced the evenness component of prey diversity (evenness in the sense of Shannon's Diversity index).

A further pattern common to all three systems was that one or a few dominant herbivore species, which were primarily limited by rainfall and/or factors related to density, supported a predator community that in turn limited the abundance of other prey species. In Kruger NP, buffalo, plains zebra, impala, and wildebeest dominated the prey biomass, and density-dependence was detected in their dynamics (Owen-Smith and Ogutu, 2003; Owen-Smith and Mills, 2006). In Serengeti NP, migratory wildebeest dominated the prey biomass and were rainfall-dependent (Campbell and Borner, 1995; Pascual and Hilborn, 1995; Mduma et al., 1999), whereas plains zebras were not (they may have been predator-limited; Grange et al., 2004). In Laikipia, plains zebra and giraffe dominated the prey biomass, and were either influenced by rainfall or by factors related to density, or both (Georgiadis et al., 2007). Other species appeared to become predator-limited following the restoration of predators.

These recurring patterns suggest that the abundance and distribution of savanna herbivores are defined not only by rainfall (East, 1984), and the relative representation of habitat types, but also by predation, both directly via consumption, and indirectly, via apparent competition (in which one or more prey species can indirectly depress others by increasing the abundance of shared predators; Holt, 1977; Holt and Lawton, 1994). The prevalence and role of apparent competition in structuring savanna prey communities, the extent to which predators affect prey dynamics other than by eating them (for example, by reducing prey birth rates; e.g. Preisser et al., 2005; Creel et al., 2007), and whether patterns of habitat association among savanna ungulates are determined not only by preference, but also by predation (as they are in N. America: Ripple et al., 2001; Fortin et al., 2005), require further scrutiny.

4.1. Conservation and management implications

Restoration of a relatively intact predator community in Laikipia District, no part of which is formally protected as a national park or reserve, amounted to a remarkable conservation success, and affirmed that pro-wildlife ranches in Laikipia District are functionally well-protected. However, given that predator restoration was not the only factor affecting ungulate populations, and that livestock dominate the herbivore biomass in Laikipia, circumspection is warranted in inferring conservation and management implications.

The presence of humans and livestock in the landscape may influence predator–prey dynamics in both direct and indirect ways. First, while the livestock subsidy of predators is negligible in years of close-to-average rainfall, subsidy may be substantial when livestock die-offs occur in years of drought and flood, as suggested by the effects of El Niño and La Niña events on livestock mortality in 1997–2001. Such episodic increases in the livestock subsidy of predators that scavenge (including lions, hyenas and leopards) may subsequently increase predation pressure on wild prey populations, at least temporarily.

Second, while predator suppression on pro-wildlife properties is today rare in Laikipia, predator suppression continued intermittently on some properties, or resumed temporarily after the drought in 2001, particularly of hyenas. This was intended not only to reduce losses of livestock, but also to reduce losses of threatened or endangered species such as hartebeest, Grevy's zebra, and oryx, which were previously abundant. Evidently, this intermittent and patchy predator suppression was insufficient to halt prey declines. The extent to which episodic subsidy of predators by livestock die-offs is balanced by intermittent predator suppression is not known.

Should it become necessary to actively conserve declining ungulate species in Laikipia District, resumption of predator suppression should not be the primary intervention. Alternatives exist, but need experimental testing. One option is to attempt indirect management solutions, such as use of fire or other means to create patches of open habitat as refugia that would facilitate detection of predators by prey (the rapidly increasing elephant population will have this effect in coming years). Another is to supplement micro-nutrients in the form of salt licks to test if nutrient deficiencies also limit herbivore recruitment. A further option is to recognize that the persistence of negatively interacting species is often achieved in nature by their spatial separation in the landscape. Threatened species can be conserved by strategic zoning, with management explicitly favoring different species in different zones. For example, ranches lacking predators, such as Solio, could be vital for hartebeest conservation. All interventions require careful monitoring to ensure they have the intended effect.

Finally, some pro-wildlife properties in Laikipia District have reduced or even eliminated cattle in order to favor wildlife. In this context, we propose a third effect of livestock that may indirectly moderate predation pressure on wild ungulates. In 2005, biomass density estimates of the dominant herbivore species in Laikipia, cattle and plains zebra, were 1.91 t km⁻² and 1.01 t km⁻², respectively. Both are mid-sized grazers, both are rainfall-limited, and zebra dynamics in Laikipia are also dependent on factors related to density (Georgiadis et al., 2003, 2007). Given that their food resources are shared, yet limiting, they are likely to be competing with each other, at least in dry years (see also Young et al., 2005). Since cattle typically do not support predators, and plains zebras in Laikipia are not predator-limited, removal of cattle may result in an increase not only of zebras, but also of their predators, and cause further declines in predator-susceptible species.

The extent to which relative abundances of predator and prey species are influenced by cattle densities needs further study. Non-lethal effects of humans and livestock on pred-

tors and wild herbivores, for example, via disturbance and displacement (Ogutu et al., 2005), are also potentially important, but little-understood. Greater understanding of these direct and indirect effects will be critical for the management and persistence of wildlife in human-occupied landscapes.

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