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Lions influence the decline and habitat shift of hartebeest in a semiarid savanna

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Efforts to restore large carnivores often are conducted with an assumption of reciprocity, in which prey populations are expected to return to levels approximating those prior to carnivore extirpation. The extent to which this assumption is met depends on the intensity of predation, which in turn can be influenced by the magnitude of environmental change over the period of large-carnivore extirpation. Recent declines of hartebeest (*Alcelaphus buselaphus*) populations in Laikipia, Kenya have coincided with recolonization by large carnivores, particularly lions (*Panthera leo*), over the past 20 years. To understand whether and the extent to which predation by lions underlies hartebeest declines, we monitored vital rates of hartebeest that were variably exposed to or protected from lions. Lion exclusion shifted rates of population growth from negative to positive ($\lambda = 0.89 \pm 0.04$ versus 1.11 ± 0.11 for control and lion exclusion zones, respectively) and, consistent with other studies on ungulate demography, adult survival was the most sensitive and elastic vital rate. Analysis of life table response experiments revealed that 32% of the variation in population growth was due to fecundity, which had the greatest proportional effects on λ. In addition, hartebeest selected open (grassland) areas more strongly where lions occurred, and avoided areas with dense tree cover. Our work provides experimental evidence to support the hypothesis that hartebeest declines have been driven primarily by lion restoration, although we cannot eliminate the possibility that predation by spotted hyenas (*Crocuta crocuta*) additionally suppressed populations of hartebeest. Given that tree cover has increased across Laikipia over the past 50 years, we suggest that lion-driven declines of hartebeest have been exacerbated by landscape change.

Jitihada za kuwarejesha wanyama wakubwa walao nyama inaambatana na dhana ya usawa ambapo viwango vya walao majani wanatarajiwa kurudi kama ilivyokuwa kabla ya kudhoofishwa kwa idadi ya wanyama wala nyama hapo mwanzoni. Uwezekano wa dhana hii unategemea kiwango cha kuuwawa cha walao nyama, jambo hili kwa upande moja pia linaweza kuathiriwa na ukubwa wa mabadiliko ya mazingira katika kipindi hicho. Hivi karibuni upungufu wa idadi ya wanyama aina ya kongoni katika eneo la Laikipia, Kenya, umefanyika kwa usanjara na kuongezeka kwa simba miaka ishirini iliyopita. Kuelewa kana kwamba kupungua kwa kongoni kumechangiwa na kuongezeka kwa kuwindwa na simba, tulifuatilia takwimu muhimu za kongoni ambao walikuwa na ulinzi kiasi au kamili kutokana na simba. Kutengwa kwa simba kulibadilisha viwango vya ukuaji wa idadi ya kongoni kutoka hasi hadi chanya ($\lambda = 0.89 \pm 0.04$ kulikokuwa na simba dhidi ya 1.11 ± 0.11 kulikotengwa simba), jambo hili ni dhabiti na matokeo ya utafiti wa demografia ya wanyama wala nyasi ambapo maisha ya wanayama wazima yalikuwa kiwango nyeti na muhimu. Uchambuzi wa matokeo ya majaribio ya jinsi maisha ya hawa wanyama yalivyo, ulibaini kuwa asilimia thelathini na mbili ya mabadiliko ya idadi yao ilitokana na uzaaji, jambo ambalo lilikuwa na madhara makubwa juu ya λ. Zaidi ya hayo, katika maeneo yaliyokuwa na simba, kongoni walipendelea zaidi mahali wazi (nyika) na kuepuka vichaka. Kazi yetu inatoa ushahidi wa majaribio na

kuitikia wazo letu kuwa kupungua kwa kongoni kumechangiwa pakubwa na kurejeshwa kwa simba. Kutokana na kuongezeka kwa miti katika eneo la Laikipia kwa kipindi cha miaka hamsini iliyopita, tunashauri kwamba kupungua kwa idadi ya kongoni kutokana na simba kumechangiwa zaidi na mabadiliko ya mazingira.

Key words: *Alcelaphus*, antelope, carnivore restoration, demography, habitat selection, savanna, sensitivity, survival, top-down control

Large-carnivore restoration often is expected to revert ecosystem properties to states approximating those prior to large-carnivore extirpation (Soulé et al. 2005; Estes et al. 2011; Ripple et al. 2014; Ford and Goheen 2015a). Carnivore restoration can be achieved through targeted reintroduction or translocation (Breitenmoser et al. 2001), or through natural recolonization of a historical geographic range in response to increased tolerance by local people (Hayward and Somers 2009; Woodroffe 2011; Chapron et al. 2014). When carnivores are restored following lengthy absences, ungulates and other prey may be naïve to the risk of predation, creating strong potential for declines of species of prey that already were rare before carnivore restoration. This phenomenon is particularly acute with secondary prey (i.e., rare species that are consumed opportunistically, and whose populations are therefore decoupled from those of carnivores; sensu Holt and Kotler 1987; DeCesare et al. 2010; Wittmer et al. 2013). Additionally, carnivore restoration may impact prey populations by inducing behavioral modifications (Brown et al. 1999; Preisser et al. 2005). For example, in the presence of large carnivores, ungulates minimize predation risk by selecting habitats to reduce their risk of detection, or by increasing vigilance (Lima 1999; Laundre et al. 2001; Caro 2005; Ford and Goheen 2015b; Donadio and Buskirk 2016), both of which can reduce food intake.

Effects of reintroduced or recolonizing carnivores on their ungulate prey range from pronounced impacts on prey numbers and behavior (e.g., Berger et al. 2001; Fortin et al. 2005; Ford et al. 2015a) to subtle or otherwise limited shifts in abundance, group size, or vigilance (e.g., Hunter and Skinner 1998; Davies et al. 2016; Moll et al. 2016). Such variable outcomes likely are a consequence of prey vulnerability and other system-specific details (Creel 2011; Gervasi et al. 2013). In African savannas, tree cover repeatedly has been demonstrated to affect predation risk, with high cover impeding detection and evasion of predators (Riginos and Grace 2008; Thaker et al. 2011; Ford et al. 2014; Riginos 2015). Therefore, tree cover may mediate the relative strength of top-down and bottom-up forcing of ungulate populations, and may be particularly influential in shaping recently restored predator-prey dynamics.

The Laikipia Plateau in central Kenya provides opportunity to examine ungulate responses to carnivore restoration. Following settlement by European ranchers in the early 1900s, livestock ranching and commercial sport-hunting were the predominant land uses in Laikipia (Denney 1972; Western and Henry 1979). During this period, livestock losses were reduced by lethal control (shooting and poisoning) of large carnivores (spotted hyenas [*Crocuta crocuta*], leopards [*Panthera pardus*], African wild dogs [*Lycaon pictus*], and especially lions [*P. leo*]). Consequently, large carnivores were greatly reduced in number, and lions were largely extirpated from most parts of Laikipia by the 1960s leading to increases in the abundance of their primary prey, plains zebra (*Equus quagga*—Denney 1972). In the 1950s (i.e., around the same time that lethal control of carnivores was highest), commercial ranchers began to suppress wildfire and prohibited local Maasai, Samburu, and Turkana tribes from controlled burning (Heady 1960; Sundaresan and Riginos 2010) thereby triggering increases in tree cover (Augustine and McNaughton 2004). During this time, some species of tree expanded into areas from which they had been absent previously (Heady 1960; Pratt and Gwynne 1977; Okello et al. 2001).

In the 1990s, lethal control of large carnivores abated as most commercial ranchers 1) adopted the use of predator-resistant enclosures (locally known as "bomas") for corralling cattle at night (Ogada et al. 2003; Woodroffe et al. 2005; Frank 2008); 2) increasingly perceived competition between zebra and cattle (*Bos indicus*) for grass; and 3) began viewing ecotourism as a potential supplement to revenues from livestock. This period, therefore, marked the beginning of attempts to conserve large carnivores alongside livestock in the region, and commercial ranchers started to tolerate lions and other large carnivores on "pro-wildlife" properties (Georgiadis et al. 2007a). Because tourism offered financial incentive to conserve large carnivores despite livestock depredation, pro-wildlife properties tolerated the recolonization of lions across landscapes occupied by people and their livestock. Currently, lion numbers on pro-wildlife properties in Laikipia are estimated at 200–250, representing a density of 6 individuals/100 km^2 (Frank 2011). These densities are comparable to protected areas (e.g., Tsavo National Park, with 4 individuals/100 km^2—Patterson et al. 2004).

Following the recolonization of lions over the past 25 years in Laikipia, many species of wild ungulates on pro-wildlife properties have declined markedly (Georgiadis et al. 2007a), including hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnus*), eland (*Taurotragus oryx*), and greater kudu (*Tragelaphus strepsiceros*). The rate and timing of these declines are similar across species, suggesting one or more common mechanisms of decline. Poaching in Laikipia is uncommon, particularly on pro-wildlife properties that maintain coordinated anti-poaching and security networks. Likewise, a 40-year time series exploring rainfall and density-dependent population regulation demonstrated that only zebra were regulated by rainfall and that only zebra and giraffes (*Giraffa camelopardalis*) exhibited density-dependence (Georgiadis et al. 2003, 2007a). Livestock populations on pro-wildlife properties have not increased over this time (Georgiadis 2011).

Georgiadis et al. (2007b) attempted to elucidate the causes of ungulate declines in Laikipia, addressing 10 alternatives,

and focusing mostly on hartebeest. They found only predation to be consistent with all available information, but the precise mechanisms of hartebeest decline remain unconfirmed. To test the hypothesis that predation—and specifically, predation by lions—underlies declines of hartebeest, we used 6 years (2009–2015) of hartebeest sight–resight data to estimate population trends, age structure, and vital rates (survival of calves, subadults, and adult females, plus adult fecundity). We also quantified resource selection by hartebeest via resource selection functions (RSFs—Boyce and McDonald 1999). We sought to answer 2 questions: 1) How do lions influence growth and vital rates of hartebeest populations? and 2) Does risk of predation from lions alter habitat selection of hartebeest? We chose to focus on hartebeest vital rates and habitat selection for the following reasons. Hartebeest have exhibited the steepest proportional declines of any wild ungulate within Laikipia over the past 3 decades (Georgiadis et al. 2007a); additionally, hartebeest appear to be preferred prey of lions on at least some properties in Laikipia (C.C. Ng'weno et al., pers. obs.). So, if predation has driven declines of populations of wild ungulates, changes in population size, behavior, or both should be detected readily for hartebeest. Additionally, hartebeest are open-grassland specialists, for which we might expect the strongest interactions between risk of predation and habitat selection (see also Moll et al. 2016).

Materials and Methods

Study site.—We conducted our study at Ol Pejeta Conservancy (OPC) in Laikipia County, Kenya, a 328-km^2 pro-wildlife property located on the equator (0°N, 36°56′E). *Acacia drepanolobium* and *Euclea divinorum* characterize the overstory of OPC. The conservancy receives approximately 900 mm rainfall annually (Birkett 2002). Within OPC, ca. 70 lions occur in 5 prides (OPC Ecological Monitoring Department, pers. comm.). Other large carnivores on OPC include spotted hyenas, leopards, cheetahs (*Acinonyx jubatus*), and African wild dogs. Other large mammals on OPC include elephants (*Loxodonta africana*), African buffalo (*Syncerus caffer*), black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), Thomson's gazelle (*Eudorcas thomsonii*), Grant's gazelle (*Nanger granti*), impala (*Aepyceros melampus*), oryx (*Oryx gazella*), Grevy's zebra (*Equus grevyi*), waterbuck, eland, plains zebra, giraffes, and hartebeest.

OPC is comprised of 2 zones with different management regimes: 1) a 294-km^2 conservation area in which cattle production occurs alongside wildlife with the full complement of large carnivores; and 2) a 32-km^2 lion exclusion zone (hereafter "exclusion zone"), constructed with the intent of bolstering numbers of declining ungulates, primarily hartebeest. Stocking rates are maintained at equal densities of 20 cattle per km^2 in both zones. Prior to construction of the exclusion zone, lions (but not other large carnivores) were captured and translocated to the conservation area (hereafter "control zone"); in the rare instances that lion incursions occur, they are removed and translocated to the control zone within OPC or to other pro-wildlife ranches. The exclusion zone is adjacent to the conservation area, and is demarcated by a 3,200-m long, 2.5-m tall solar-powered electrified (6,000–7,000 V) fence with 9 strands spaced 0.2-m apart. The fence is fortified with chain-link 1.50 m above and 0.60 m beneath the ground. The 2 zones have comparable grass biomass (ca. 1,500 kg/ha) and water availability (OPC Ecological Monitoring Department, pers. comm.).

In each of 4 years (2012–2015), we conducted camera-trap surveys to assess densities of large carnivores in control and exclusion zones. We divided OPC into 3 blocks (northern, southern, and eastern) of comparable area, overlaid a 2 × 2 km grid over each block, and sampled each block for 21 consecutive days between the months of October and December. A single camera trap (Reconyx Rapidfire RM45; Reconyx, Holmen, Wisconsin) was deployed at the center of each grid cell to ensure uniform distribution of sampling points. This yielded 1,512 camera-trap nights (72 traps × 21 days) per year. We deployed cameras within 50 m from the centroid of each grid cell, typically near active game paths to maximize captures. We mounted cameras on trees or metal cages 3 m from game paths at 45 cm above the ground, and checked them every 7 days to ensure continuous operation. After 21 days, we removed cameras, downloaded images, and calculated density estimates for lions, spotted hyenas, and black-backed jackals (*Canis mesomelas*) according to Carbone et al. (2001). Leopards, cheetahs, and African wild dogs were photographed too infrequently to calculate densities. Densities of spotted hyenas within the exclusion zone were approximately 70% of the control zone; densities of black-backed jackals were not statistically distinguishable between zones (Supplementary Data SD1; OPC Ecological Monitoring Department, pers. comm.).

Hartebeest and lion surveys.—Hartebeest are pure grazers that form distinct herds; a strong dominance relationship between females defines the social organization of each herd (Kingdon 1982). They calve throughout the year in accord with rainfall variability. At OPC, hartebeest occur in herds of up to 15 individuals that defend small territories (< 5 km^2) from conspecifics. From 2009 to 2015, we conducted twice-monthly drive transects to quantify population densities of hartebeest in within our study area. Beginning in 2012, we included sight–resight methods on drive transects to estimate demographic rates and age structure of herds within both zones (Skalski et al. 2005; see also Supplementary Data SD2). We conducted surveys with 2 observers and a driver from 0800 to 1100 h (n = 17, mean distance per transect = 7.50 km ± 0.84 *SE*). Surveys of the exclusion zone took 1 day, whereas the control zone was surveyed in 3 consecutive days. Upon sighting a herd, we approached from the downwind side to within a distance of about 150 m, and then would spent 10–15 min habituating the herd before gradually moving to ca. 70 m to avoid disturbing the animals. During these 2 stops, we estimated the bearing to the herd using handheld compasses. We determined the radial distance from the point where the center of the group was initially sighted to the nearest meter using a laser rangefinder. Lastly, we marked the location of observations using handheld GPS units. We used binoculars to clarify

group size, and the sex and age classes of individuals within the herd. Individuals were categorized as 1 of 3 age classes using a suite of characteristics, including size, body shape, and horn shape and development (Andanje 2002; Supplementary Data SD3): calves (0–12 months), subadults (13–23 months), and adults (≥ 24 months). Individuals were considered to belong to the same herd when the distance between them was less than 60 m. Our methods adhered to ASM animal care and use guidelines (Sikes et al. 2016).

We estimated abundance of lions by radiotracking 5 dominant lionesses from each of the 5 established prides within OPC, fitted with radiocollars. Lions were captured and collared with the assistance of a Kenya Wildlife Service veterinary team using protocols described by Frank et al. (2003). Lions were darted from a parked field vehicle at a distance of 10–30 m with a 2-ml dart containing a combination of ketamine (0.2 mg/kg), medetomidine (0.03 mg/kg), and atipamezole (0.33 mg/kg) using a CO_2 rifle (Dan-inject RSA, Skukuza, South Africa). Lions were then reversed and observed until they were able to walk and rejoined other pride members. From 2009 to 2011, VHF collars (Telonics, Mesa, Arizona) were used and later replaced in 2012 with GPS collars (Vectronics Aerospace GmbH, Berlin, Germany). Because lions live in stable social units (prides), collars allowed regular resighting of uncollared individuals within prides, allowing for weekly monitoring. We obtained additional data from sightings and photographs by safari guides and clients operating within the conservancy (see Supplementary Data SD1). We estimated abundance of lions from weekly monitoring of known individuals, during which all lions were individually identified using whisker-spot patterns, scarring, and tooth breakage (Pennycuick and Rudnai 1970; Becker et al. 2013).

We fit generalized linear models (GLMs) to explain hartebeest densities in the control zone using the following predictor variables: 1) lion density, estimated by resighting of uniquely identifiable individuals from whisker spots (see below); 2) rainfall, collected from 10 stations distributed throughout OPC; and 3) population size of hartebeest in the control zone from the previous year. We constructed a suite of candidate models and calculated each model's AIC_c (Akaike Information Criterion, corrected for small sample sizes) and AIC_c weights (W_i) as a metric for strength of evidence to compare the performance of each model (Burnham and Anderson 2002). These statistical analyses were conducted in Program R version 3.2.3 (R Development Core Team 2015) using package MASS (Venables and Ripley 2002).

Demographic analysis.—We calculated age-specific survival (calf survival [S_c], subadult survival [S_{sa}], and adult survival [S_{ad}]; Supplementary Data SD4) from October (t) to September of each subsequent year ($t + 1$) for 288 individuals in 15 herds between 2012 and 2015 using the "survival" package in R (Therneau 2012). To calculate fecundity (F_a), we used estimates of the number of calves produced per year per adult female (calves/adult female * S_{ad}), and assumed an equal sex ratio of offspring following Sinclair et al. (2003). Female hartebeest are philopatric, and remain within the maternal herd for life (Gosling 1974). Males begin dispersing at about 20 months (Kingdon 1989). Hence, we were able to identify individuals from when they were first observed until they either were recruited to the subadult age class or disappeared. We equated disappearance (lack of detection in 6 consecutive sight–resight surveys over the course of 3 months; see *Hartebeest surveys*) with mortality. Hartebeest have an 8-month gestation period, and gravid females were noticeable at 5 months with swollen bellies. We observed calves for 94.3% of gravid adult females in the control zone, 96.3% of gravid adult females in the exclusion zone (Supplementary Data SD5).

We constructed 3 × 3 age-structured post-birth pulse matrix models to estimate population growth rate (λ) in each zone, and determined sensitivity and elasticity of λ to individual vital rates (Caswell 2001; Owen-Smith and Mason 2005). To discern vital rates with the greatest impact on differences in λ between control and exclusion zones, we performed a life table response experiment (LTRE—Caswell 2000; Maclean et al. 2011; Supplementary Data SD6). We calculated 1) the difference in λ between the zones ($\Delta\lambda = \lambda_{Exclusion} - \lambda_{Control}$); and 2) contributions of each vital rate toward this difference for the period 2012–2015 using averaged estimates of vital rates. LTREs and other retrospective analyses identify the demographic variables that have, in the past, contributed most to observed variation among populations in λ (Caswell 2001).

Analysis of habitat selection.—We quantified habitat selection using selectivity measures (Manly et al. 2002). We characterized habitat types based on tree cover according to GIS layers ground-truthed and digitized from a landsat ETM7 satellite image by Birkett (2002): 1) dense bushland (> 50% overstory cover dominated by *E. divinorium*); 2) open bushland (10–30% overstory cover dominated by *A. drepanolobium*); and 3) open grassland (mostly treeless areas, with understory cover dominated by *Themeda triandra*, *Pennisetum stramineum*, and *P. mezianum*). From studies in similar systems (e.g., Hopcraft et al. 2005; Valeix et al. 2009; Ford et al. 2014), we believed dense bushland, open bushland, and open grassland would be correlated with high, intermediate, and low levels of risk of predation, respectively. For each hartebeest herd, we constructed minimum convex polygons (MCPs—Mohr 1947), with 95% of the locations to delineate habitat availability using ArcGIS 10.3 (ESRI 2013). We then generated random points and sampled availability using a 1:1 ratio of used to available locations within the MCP. For all used and random points, we measured habitat use and availability with a population level design in each zone (control zone: n = 1,806 used locations [herd sightings]; exclusion zone: n = 857 used locations—Boyce and McDonald 1999; Manly et al. 2002; Boyce 2006). We described habitat selection as differences in observed use to expected availability of habitat type using selection ratios, and tested preference or avoidance for each habitat using a log-likelihood chi-square test for overall habitat selection. Selection ratios greater than 1.0 indicated positive selection for a habitat type and ratio values less than 1.0 indicated a selection against habitat type. We used the adehabitatHR package in R to analyze habitat selection (Calenge 2014).

Results

From 2009 to 2015, population size of hartebeest in the exclusion zone increased while it declined in the control zone (Fig. 1), and the GLM containing only lion abundance was the most plausible model for population density of hartebeest in the control zone through time (Table 1). In both exclusion and control zones, survival of adults was higher than survival of subadults and calves ($\chi^2_2 = 77.3$, $P < 0.001$; Fig. 2), which were statistically indistinguishable (exclusion zone: $\chi^2_1 = 2.2$, $P = 0.134$; control zone: $\chi^2_1 = 0.2$, $P = 0.696$). Except for survival of adults, all other vital rates were significantly higher in the exclusion zone than in the control zone (calf survival: $\chi^2_1 = 25.7$, $P < 0.001$; subadult survival: $\chi^2_1 = 18.4$, $P < 0.001$; adult survival: $\chi^2_1 = 2.9$, $P = 0.09$; fecundity: $F_{1,10} = 0.16$, $P < 0.001$; Fig. 2). Exclusion of lions bolstered population growth of hartebeest ($F_{1,4} = 12.87$, $P = 0.023$; control zone: $\lambda = 0.89 \pm 0.04$; exclusion zone: $\lambda = 1.11 \pm 0.11$), principally through fecundity and survival of adults but also through survival of calves and subadults (Fig. 3).

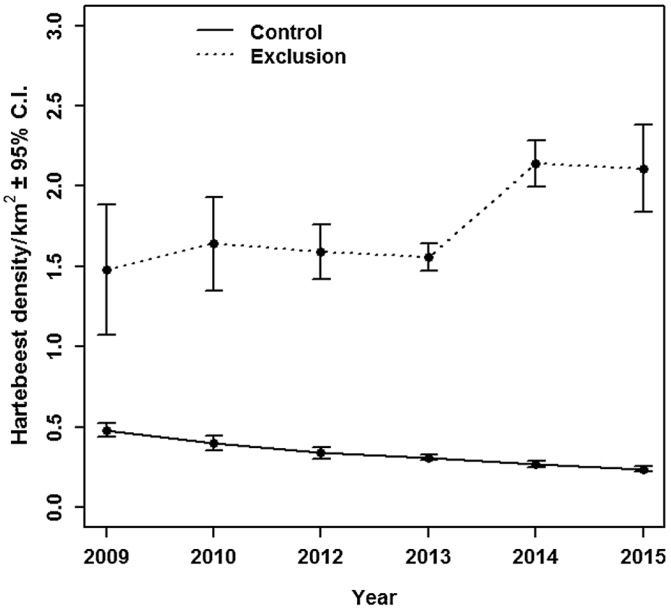

Fig. 1.—Observed time series of counts of hartebeest (*Alcelaphus buselaphus*) on Ol Pejeta Conservancy, Kenya (2009–2015). Error bars represent 95% *CI*s based on *SE*s calculated through variance estimators in Skalski et al. (2005).

Table 1.—A priori models (generalized linear model, Gaussian family) for factors influencing hartebeest (*Alcelaphus buselaphus*) population densities at Ol Pejeta Conservancy, Kenya (2009–2015).

Selected models	k	ΔAIC_c	W_i	R^2
Lion numbers[a]	2	0.00	0.97	0.73
Hartebeest density ($t-1$)	2	7.94	0.02	0.15
Rainfall	2	8.73	0.01	0.05
Lion numbers + rainfall	3	13.63	0.00	0.68
Lion numbers + hartebeest density ($t-1$)	3	13.93	0.00	0.66
Rainfall + hartebeest density ($t-1$)	3	16.60	0.00	0.51
Lion numbers * rainfall	4	41.78	0.00	0.94
Lion numbers * hartebeest density ($t-1$)	4	44.52	0.00	0.91
Lion numbers * rainfall * hartebeest density ($t-1$)	5	54.89	0.00	0.61
Rainfall * hartebeest density ($t-1$)	4	57.67	0.00	0.42

[a]$AIC_c = 66.49$.

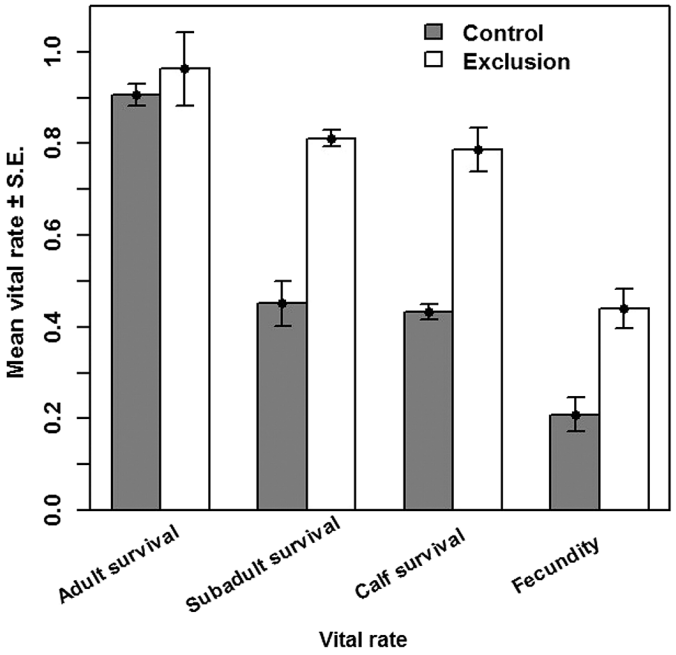

Fig. 2.—Survival rates (mean ± *SE*) of 3 age classes of hartebeest (*Alcelaphus buselaphus*) within control and lion (*Panthera leo*) exclusion zones at Ol Pejeta Conservancy, Kenya (2009–2015).

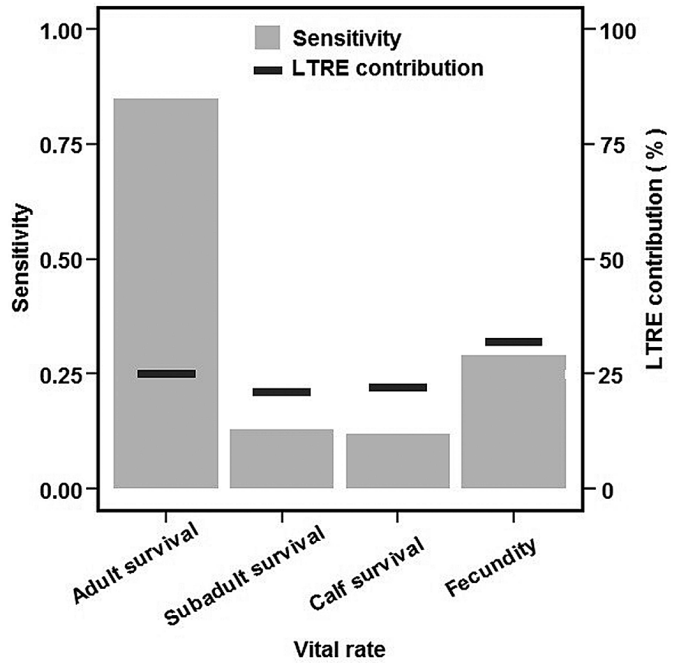

Fig. 3.—Life table response experiment (LTRE) showing demographic sensitivity and percentage contribution of vital rates (2012–2015) to change in population growth (λ) in hartebeest (*Alcelaphus buselaphus*) in paired exclusion versus control zones.

Habitat selection of hartebeest varied with the occurrence of lions (Fig. 4). In the presence of lions, hartebeest selected open grasslands (selection ratio = 1.50, 95% *CI*: 1.44–1.56) and avoided dense (selection ratio = 0.48, 95% *CI*: 0.40–0.56) and open (selection ratio = 0.69, 95% *CI*: 0.64–0.74) bushland. In contrast, there was weak evidence for selection for all 3 habitat types where lions were absent ($\chi^2_2 = 1.811$, $P = 0.404$).

Discussion

Our work contributes to growing recognition that predation is a major factor in driving population dynamics and behavior of savanna ungulates, particularly numerically subordinate species (Owen-Smith et al. 2005; Thaker et al. 2011; Grange et al. 2015; Riginos 2015). Specifically, survival rates of hartebeest calves and subadults were suppressed by lion predation, and lions triggered stronger selection for open habitats characterized by higher visibility. At least with respect to hartebeest on OPC, our work affirms the inferences of Georgiadis et al. (2007b) with direct evidence implicating predation as the cause of decline, and significantly extends them through several key findings. First, we experimentally identified a demographic pathway (reduced fecundity) through which predation suppressed population growth of hartebeest. Second, we isolated the role of a recently recolonized large carnivore (lions, and perhaps spotted hyenas to a lesser extent) in ongoing declines and projected rates of population growth of hartebeest. Finally, we demonstrated large carnivore-mediated shifts in habitat selection, whereby hartebeest are more likely to use ostensibly risky habitats following lion exclusion.

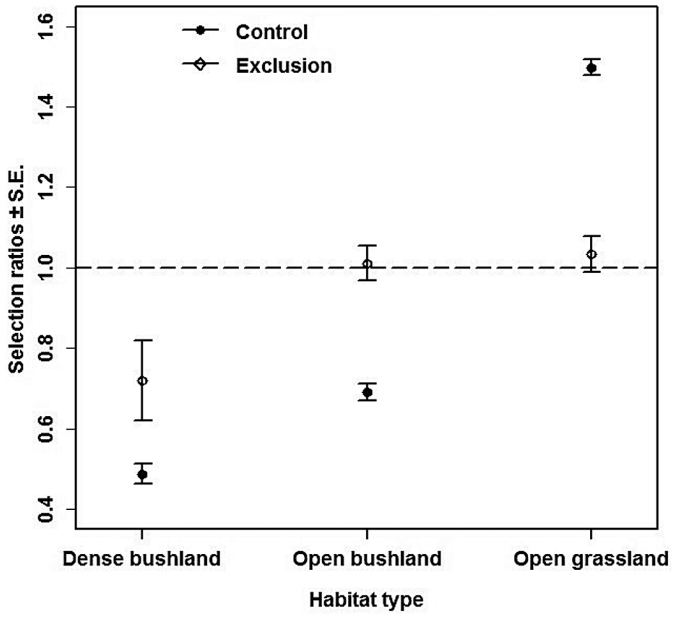

Fig. 4.—Selection ratios for hartebeest (*Alcelaphus buselaphus*) in 3 habitat types with *SE* of the selection ratio. Selection is estimated from hartebeest locations at Ol Pejeta Conservancy, Kenya (2009–2015). Selection ratios > 1 indicate preference, whereas < 1 indicate avoidance. Error bars indicate 95% *CI*s.

Although OPC represents a single property within Laikipia County, we believe our findings are representative of many properties on which hartebeest and lions co-occur. Nonetheless, we cannot rule out other potential drivers, which may exacerbate or altogether replace predation in underlying region-wide population declines of hartebeest. Increasingly, wildlife in African savannas is being compressed into ever-dwindling areas; it is possible that the aggregations of wild ungulates on Ol Pejeta have concentrated hunting by lions and other predators into the few habitats suitable for hartebeest (see also Ali et al. 2016). Additionally, severity of droughts has increased in Laikipia since the mid-1970s (Ogalleh et al. 2012). On a neighboring property, rainfall and hartebeest activity are negatively correlated (Kimuyu et al. 2016), although the degree to which increasing drought has caused population declines of hartebeest is unknown. Finally, in addition to its potential role in increasing risk of predation, tree encroachment might reduce nutritive quality of grasses, thereby reducing recruitment of hartebeest and other ungulates (Riginos et al. 2015; Proffitt et al. 2016).

For large mammals, survival of adults typically has the largest potential effect on population growth (i.e., λ is highly sensitive to small changes in adult survival—Gaillard et al. 2000). Additionally, LTRE analysis revealed that lions impacted population growth of hartebeest through all 4 vital rates, in contrast to several studies on temperate ungulates in which predators typically influence population growth mainly by suppressing survival of calves (Eberhardt 1977, 2002; Gaillard et al. 1998, 2000; Gaillard and Yoccoz 2003; Owen-Smith and Mason 2005; Raithel et al. 2007). Notably, lions suppressed population growth by reducing fecundity, which may be attributable to effects of predation as a result of 2 pathways: predator-induced stress and predator-induced shifts toward less nutritious forage. Although it has not been documented in tropical ungulates, predator-induced stress has been demonstrated to reduce reproduction in elk (*Cervus elaphus*—Creel et al. 2007, 2009), snowshoe hares (*Lepus americanus*—Sheriff et al. 2010, 2015), and common voles (*Microtus arvalis*—Jochym and Halle 2013). For example, cow elk can enhance their survival by making reproductive or behavioral trade-offs in the presence of wolves (Creel et al. 2007). Similarly, predators may trigger shifts in forage selection that are accompanied by nutritional costs. Elsewhere in Laikipia, risk of predation from African wild dogs and leopards cause impala to forage on thornier, less-preferred trees (Ford et al. 2014; see also Fortin et al. 2005). Whether reduced fecundity of hartebeest is an outcome of lion-induced stress, lion-induced shifts in habitat, or both remains a hypothesis for testing in the future.

Animals must balance food availability and predation risk when selecting habitat, and bushland habitats appear riskier than open grassland for hartebeest. Elsewhere in sub-Saharan Africa, wooded areas provide more cover for lions and other large carnivores to hunt (Hopcraft et al. 2005; Thaker et al. 2011; Loarie et al. 2013; Ford et al. 2014). In our system, hartebeest shifted their activity toward areas with higher visibility (open grasslands) in the presence of lions, suggesting that perceived risk of predation is at least partly responsible for

driving the distribution of hartebeest across landscapes (Lima and Dill 1990; see also Donadio and Buskirk 2016). To the extent that such nonconsumptive effects translate to reduced survival, fecundity, or both for hartebeest, declining populations of hartebeest in Laikipia are likely the outcome of a combination of direct (density-mediated) and indirect (behaviorally mediated) effects of recolonizing lions. The relative impact of density- versus behaviorally mediated effects of lions and other predators on hartebeest declines represents another open question for future research.

Predator restoration can inject optimism into conservation efforts typically characterized by reactive, stopgap measures. Ecologists tend to treat predator restorations as "natural experiments," a view that downplays changes in environmental conditions that may have occurred during predator extirpation. Through experiments in other systems, we know that predators can have variable effects at different times (Young et al. 2005; Stier et al. 2013) and in different places (Paine 1966), so our ability to predict the impacts of their restoration should depend on environmental context (Agrawal et al. 2007; Gervasi et al. 2013; Middleton et al. 2013). Although our work points to lions in limiting contemporary populations of hartebeest, both species co-occurred for millennia in Laikipia, so it is unlikely that lions are solely responsible for continued declines of hartebeest at OPC and elsewhere in this region. Because hartebeest typically are open-grassland specialists, and because wooded areas in Laikipia have expanded with fire suppression since the 1950s, we suggest that hartebeest (and possibly other ungulates comprising secondary prey for lions) have declined because of intensified predation. We suspect that this intensified predation itself is a combination of recent recolonization of a large carnivore (lions) to a bushier landscape in which hartebeest are rendered more vulnerable than they have been historically, and possibly because lions increasingly are excluded from pastoral land (Oriol-Cotterill et al. 2015). Consequently, we recommend that wildlife managers incorporate range restoration (e.g., prescribed fire, manual bush clearing, and other practices that promote grass growth) into efforts to conserve lions and their native prey in landscapes that have been impacted by human activities.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Densities of large carnivores within control and lion (*Panthera leo*) exclusion zones at Ol Pejeta Conservancy, Kenya based on camera-trap surveys from 2012 to 2015. Additionally, lion density based on ground survey.

Supplementary Data SD2.—Hartebeest (*Alcelaphus buselaphus*) at Ol Pejeta Conservancy, Kenya showing unique marks used to identify individuals and herds (deformed right horn [A]; notch in the upper left ear [B]; missing left horn [C]).

Supplementary Data SD3.—Illustration showing on how to distinguish hartebeest (*Alcelaphus buselaphus*) age categories, based on horn development (modified from Andanje 2002).

Supplementary Data SD4.—Three-age-structured life cycle graph of hartebeest (*Alcelaphus buselaphus*) that depicts transitions from calf (0–12 months), to subadult (13–23 months), to adult (≥ 2 years of age). In the life cycle graph, arcs that point to the same node indicate the probability of surviving and remaining in the same stage, while the other arc represents the probability of surviving and fecundity. Age-specific survival (calf survival [S_c], subadult survival [S_{sa}], adult survival [S_{ad}]), and fecundity (F_a), following Caswell (2001).

Supplementary Data SD5.—Number of pregnancies and detections of hartebeest (*Alcelaphus buselaphus*) noted within each treatment every biological year (2012–2015) and births (% of individuals giving birth, given pregnancy).

Supplementary Data SD6.—Change in mean vital rates, sensitivity, elasticity, and life table response experiment (LTRE) contribution for analyses of population growth of hartebeest (*Alcelaphus buselaphus*) in paired exclusion versus control zones for 2012–2015.

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