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EDITED BY
Robert A. Montgomery,
University of Oxford, United Kingdom

REVIEWED BY
Vicente Urios,
University of Alicante, Spain
Christian Kiffner,
Leibniz Centre for Agricultural Landscape Research (ZALF), Germany

*CORRESPONDENCE
Laurence G. Frank
✉ lgfrank@berkeley.edu

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Twenty years of lion conservation in a commercial rangeland

Laurence G. Frank[1,2]*

[1]Museum of Vertebrate Zoology, University of California, Berkeley, Berkeley, CA, United States, [2]Mpala Research Centre, Nanyuki, Kenya

Lion populations in Africa declined precipitously in the twentieth century outside of protected areas but the commercial cattle ranches of Laikipia County, Kenya, have been a unique exception, with low livestock stocking rates, careful range management, large populations of wild ungulates, and a full complement of large carnivores, including lions at a stable density of about 6/100 km^2. The Laikipia Predator Project, later Living With Lions, started in 1997 with two primary objectives: improving livestock husbandry to reduce lion predation losses and subsequent killing of lions, and studying behavioral adaptations of lions to human activities and persecution. We initially interviewed ranch owners and managers on lion numbers, losses to all mortality factors, husbandry methods, costs, and lion control measures. Studies of husbandry and control methods led to improved livestock management, which gradually reduced losses and retaliatory lion killing. Persecuted lions are secretive and nocturnal, so behavioral research was dependent upon radio collaring, requiring development an effective capture technique. Collars introduced ranchers to their lions as individuals, decreasing their propensity to shoot them after livestock predation. The most important breakthrough was the development of "lion-proof" mobile bomas (corrals) which dramatically reduced night time losses and retaliatory killing. Global positioning system (GPS)-Iridium collars for research into lion movements, allowed development of a Lion Early Warning System to inform ranchers of morning lion locations, allowing them to avoid lions during day time grazing. These measures reduced retaliatory lion killing by 90% between 1998 and 2017. Development of simple and inexpensive hyena-proof bomas for traditional pastoralists dramatically reduced their losses and motivation to poison predators. Studies of lion movements and ecological energetics in relation to human activities have revealed patterns of diel avoidance of humans/livestock by day and predation of wild prey near bomas at night, showing that lions partition their activities temporally in order to utilize high quality hunting habitat while minimizing risk of encountering humans. Studies of predation ecology suggest that lion predation does not have a significant impact on Laikipia's important population of endangered Grevy's zebra. Several other carnivore research and conservation projects in Kenya arose out of the initial work in Laikipia.

KEYWORDS

Kenya, Laikipia, livestock management, hyena, ranching, depredation, conservation, Grevy's zebra

Introduction

History of recent lion conservation

For decades, the abundance of African lions in national parks distracted conservationists' attention from their rapid decline in non-protected areas until the seminal papers by Chardonnet (2002) and Bauer and van der Merwe (2004) on continent-wide population estimates alerted the world that wild lions had undergone severe decline. Riggio et al. (2013) estimated that lions are currently found in only 17% of their historic African range, and the most recent IUCN Red List Assessment stated that "we have greater confidence in an estimate of closer to 20,000 lions in Africa than in a number over 30,000" (Bauer et al., 2017). In most countries, protected areas are too small and too widely separated to provide long term protection for viable populations of wide ranging animals like lions and elephants (*Loxodonta africana*), which conflict with humans and then suffer retaliatory killing when they move outside park boundaries (Woodroffe and Ginsberg, 1998). Growth of human and livestock numbers, decreasing tolerance for predation on livestock, as documented by rapid and widespread increase of lion killing among pastoralists (Ogutu et al., 2005; Frank et al., 2006, 2011; Hazzah et al., 2009), and increasing use of readily available cheap agricultural pesticides to poison predators caused rapid decline of lions and spotted hyenas outside of protected areas, and vultures nearly everywhere (Frank et al., 2011; Ogada et al., 2016). Without viable reproducing populations in the unprotected livestock rangelands which separate protected areas, park populations are vulnerable to stochastic events such as disease outbreaks, political unrest, and invasion by herders, who kill predators in the wake of livestock predation. As predators declined, traditional herding practices relaxed, e.g., assigning children rather than young men as herders (Hazzah et al., 2009; Kissui et al., 2022) and construction of less secure bomas, which left livestock more vulnerable to remaining carnivores and thus to more retaliatory killing.

An exception to the continent-wide decline in lion numbers outside of protected areas has been the twenty-five privately owned commercial beef ranches of Laikipia County, Kenya. These may be the only commercial livestock operations in the world today which not only tolerate large carnivores among their livestock, but even go to expensive lengths to sustain them by protecting livestock rather than killing predators. In 1997, I was asked to assess large carnivore numbers and ecology in Laikipia (Frank, 1998). Because most landowners were committed to wildlife and habitat conservation but also made their living raising livestock, they were strongly supportive of further research on lions, and particularly on reducing lion predation on cattle. In fact, most ranchers wanted more lions, as long as livestock losses did not increase.

The great majority of earlier research had focused on lion behavior and ecology in protected areas, where they are habituated to vehicles and readily observable. Little was known about lion behavior in the vast unprotected, human-dominated landscapes of Africa, where they are under pressure from humans, either by retaliatory killing in response to predation on livestock or by trophy hunting. While there had been substantial anthropological and archeological research on African pastoralism, there had been little research on minimizing livestock losses to predators. Thanks to the enthusiastic interest and cooperation of ranchers, Laikipia presented an opportunity to investigate both livestock protection and lion behavioral response to human activities and disturbance, including lethal control.

This paper summarizes research by the Laikipia Predator Project, the name of which was subsequently changed to Living With Lions (LWL) when we added additional projects in the unprotected regions around Amboseli National Park and in the Mara conservancies, both in Kenya's Maasailand. These are ecologically and socioeconomically distinct landscapes without formal wildlife protection, in which cattle production, either commercial or subsistence, was the traditional economic base. Although tourism has grown in importance in all three areas, practical knowledge gained about both lions and livestock protection is potentially generalizable to livestock rangelands throughout sub-Saharan Africa.

This paper is a retrospective on an early and influential effort to address the central conservation problem of lion-livestock conflict, practical solutions to which are critical to the persistence of viable lion populations outside of parks. The Laikipia work started with a survey of ranchers, covering many aspects of their interactions with lions, the other five species of large carnivores, and four species of livestock; their experience informed subsequent research on livestock management to prevent predation losses. Studies of lion behavior in relation to human and livestock disturbance have demonstrated complex responses which allow lions to minimize dangerous interactions with humans by day while still allowing them to access wild prey at night. As originally intended in 1997, Laikipia has proven to be a fruitful laboratory in which to investigate and improve coexistence between humans, their livestock, and large carnivores.

The Laikipia landscape

Laikipia County is 9,663 km^2 in size and lies on the equator in central Kenya. It is the highly biodiverse ecotone between the mesic grasslands to the south and the semiarid *Acacia (Vachellia)* spp., bush savanna of northern Kenya and the Horn of Africa. Rainfall is low, 400–800 mm annually in two rainy seasons, and although southern Laikipia near Mt. Kenya is suitable for both large and small scale agriculture, a strong rainfall gradient and poor soils make semiarid central and northern Laikipia economically suitable only for livestock production or conservation and tourism.

Most fences within and between ranches (Denney, 1972) had been removed when a resurgent elephant population made maintenance impossible, and wildlife are free to move, both within Laikipia and to undeveloped regions to the north. Most wildlife-friendly ranches are contiguous and comprise 3,576 km^2, ranging in size from 10 to 386 km^2, with a mean of 132.4 + 20.1 km^2 (SE). They raise primarily cattle, but also small numbers of sheep and goats (shoats) and camels. Most maintain low stocking densities of cattle, about 1 per 8 ha, and thus still support healthy, productive grasslands. Wildlife is diverse and abundant, with large populations of grazing and browsing ungulates characteristic of both grassland and bush savanna (Georgiadis et al., 2007). The ranches, many of which have become formal conservancies in recent years, comprise 38% of Laikipia, **Figure 1**, and support most of its wildlife; many

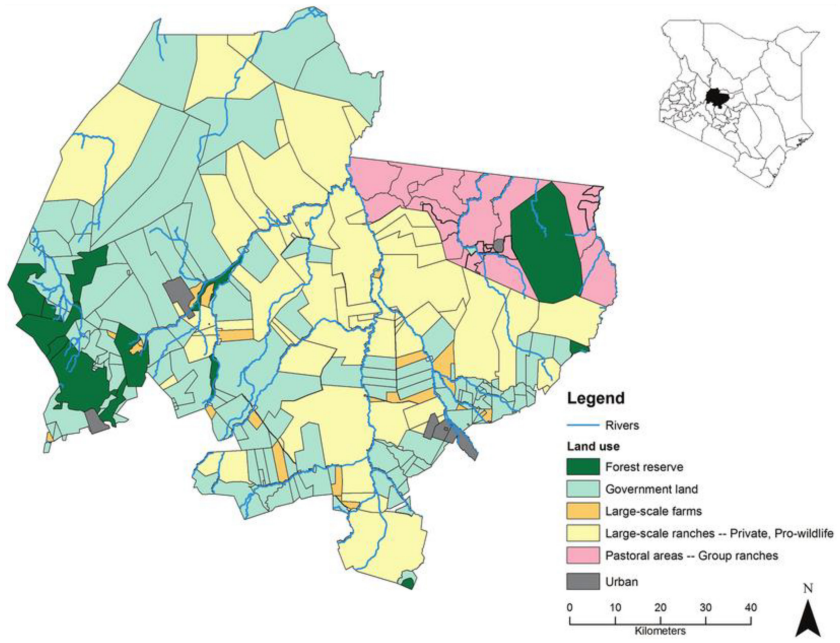

FIGURE 1
Land use patterns of Laikipia County, Kenya. Most wildlife occurs on the large scale commercial ranches/conservancies, government land is occupied by smallholder farmers or pastoralists, group ranches are communally owned pastoralist communities, the forest reserves are heavily grazed by pastoralists.

now host small upscale tourism operations to supplement cattle income and one supports mass tourism. All border communal lands. Four are owned by wealthy foreigners, most of the rest by families which settled in the early years of the 20th century. Four are currently owned by international conservation Nongovernmental Organization (NGO)'s.

Roughly 10% (1,000 km^2) of Laikipia comprises densely populated, communally owned "group ranches" of traditional pastoralists, mostly Laikipiak Maasai, practicing traditional subsistence pastoralism. These lands are badly degraded from heavy overgrazing by high numbers of livestock and by charcoal burning, and have become marginal for cattle, leaving goats and sheep as the primary livestock. Wildlife is sparse, predator poisoning is common (Frank et al., 2011), raptors and vultures have declined steeply (Ogada and Keesing, 2010) and few if any lions are resident.

Colonial period

As elsewhere in the world, Laikipia ranchers were not always tolerant of predators. For much of the 20th century, predators were shot on sight by ranchers and Game Department wardens: between 1946–1952, one Laikipia game warden shot 434 lions "on control" (Herne, 1999). Poison (strychnine and organophosphate cattle dips) was widely used on East African ranches to control predators, continuing well into the latter half of the twentieth century (Denney, 1972). Both the Kenya Wildlife Service and the Kenya Veterinary Department still poisoned spotted hyenas (*Crocuta crocuta*) on a wide scale until this century, killing lions and other scavengers as well (Kenya Wildlife Service, 1997; Frank, pers. obs, 1991). In the 1990's, at least one ranch still used poison, to the dismay of other property owners; it subsequently changed hands and poisoning ceased. In the 1970's and 80's, one Laikipia rancher and a colleague shot over 300 lions apiece in the course of experimental ranching in a vast, remote part of NE Kenya (Anon., pers. comm.). Thus, tolerance of large carnivores is a relatively recent phenomenon, partly a result of growing tourism, but also driven by the recognition that African wildlife is in rapid decline and that private landowners have the interest, and often greater capacity than government, to maintain even problematic species like lions and elephants.

The current landscape and mix of wildlife certainly does not duplicate that prior to colonization and fire suppression. Early accounts and older residents report that there was more open grassland and less bush in the first part of the twentieth century, as the Maasai practiced annual burning while subsequent European settlers suppressed fire. There were more grazers such as hartebeest (*Alcelaphus buselaphus)*, Thomson's gazelles (*Eudorcas thomsonii)*, and warthogs (*Phacochoerus africanus*), which have declined markedly with transition to bush, and fewer browsers; elephants were virtually non-existent in Laikipia in the 1920's but with protection and conversion of grassland to bush savanna, today there are over 6,000. In these productive grasslands, wild ungulates and large carnivores would have been more abundant than today.

Lions and livestock: costs and management

Initial survey

Research on Laikipia lions commenced in 1997 by interviewing owners or managers of 20 commercial ranches, with properties

FIGURE 2
Traditional Maasai manyatta, showing outer fence of thorn bush surrounding smaller internal bomas and dwellings. A thorn boma on a commercial ranch in Laikipia was a single unit, often divided into "rooms," with herder dwellings outside the perimeter.

amounting to 2,789 km^2, 78% of the wildlife friendly area, and eight community elders. Because the communal lands do not support resident lions, the primary focus was on the ranches. I asked nearly 700 rather repetitive questions on the relationships between each livestock and each predator species, including losses to all mortality factors, estimated predator and exact livestock numbers, predator control measures, overall operating costs, and the costs of protecting livestock from predation by each predator species (Frank, 1998). I did not attempt to quantify less tangible non-monetary costs of tolerating predators described by ranchers. These include grazing time (and thus weight gain) lost while livestock were in bomas rather than grazing at night, or time spent by herders and security staff rounding up scattered stock after a lion attack had caused a stampede. Nor was it possible to quantify the positive impact of lions; there was little tourism in Laikipia in 1997 but ranchers frequently expressed their love, respect, and appreciation for African wildlife, African people, and the Laikipia landscape.

Commercial ranches in Kenya used traditional African livestock husbandry methods, close herding by day and confinement in thorn bush bomas at night. A Samburu or *Maasai manyatta* (settlement) belongs to one adult man and consists of a large thorn bush perimeter boma inside of which each wife has her own hut (**Figure 2**). Smaller bomas within the outer wall contain his livestock at night, and dogs are kept to warn of approaching predators or human raiders. Ranches use a similar layout, with herders sleeping in huts next to the boma, and many properties employ a night guard to stand watch. When predators are detected near a boma, herders chase them off with bright lights and noise, or sometimes shotgun blasts at the sky. Each ranch had a number of permanent bomas spread across the property and livestock were moved between them every few months as grazing and water availability changed.

Lions typically take cattle by approaching a boma at night, causing them to panic and stampede through the boma wall. Lions take one or more, others are often taken by spotted hyenas in the bush, and herders spend the following day tracking down strays. To effectively contain stampeding cattle, a thorn boma needs to be made either of stout, dense shrubs or substantial trees, and requires regular maintenance to replace rotted materials, leading to gradual local deforestation. A few were made of stone topped with barbed wire, or surplus cedar posts left over from earlier fencing, forming a solid stockade. Bomas on communal pastoralist lands tended to be flimsy due to long term degradation of woody vegetation for boma construction, firewood, and widespread commercial but illegal charcoal production.

Predation on livestock

On commercial ranches, 0.8% of cattle and 2.1% of sheep and goats were lost annually to lions in 1995–1996 (**Figure 3**), including those killed by hyenas after lions stampeded them out of bomas. By comparison, disease killed 2.5 and 8.2%, respectively. Note that only

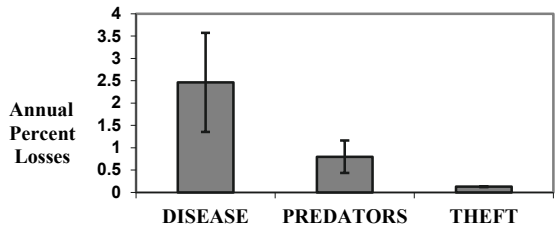

FIGURE 3
Percent (+ SE) of cattle lost to disease, predators, and theft on twenty commercial ranches in Laikipia, 1995–1996 (F = 7.85; df = 2.37; p = 0.0014).

one ranch raised large numbers of sheep and it sustained high losses to lions. Pastoralist group ranches sustained very similar losses, 0.9% of cattle and 2.5% of sheep and goats; no data on losses to disease and theft were available for communal lands. Ranch losses to theft were low, but livestock production would not be possible without bomas and vigilant herding and security staff.

Seasonality

Both ranchers and pastoralists reported that lions were more likely to take livestock during the rainy season and subsequent research supported this (Frank, 1998; Frank et al., 2005; Woodroffe and Frank, 2005). We recorded one lion shot during the drought year of 2,000 and 12 shot or trans-located after the rains returned in 2001. We speculate that listless wild prey and ready availability of carcasses during dry periods provide easy meals and that lions are likely to turn to livestock when abundant grass makes well-nourished, alert, and energetic wildlife more difficult to hunt successfully.

Bomas

Twenty-eight percent of losses occurred by day when herds inadvertently encountered resting lions while grazing, and ranchers considered these attacks to be nearly unavoidable. Night time losses occurred in two circumstances: when herders inadvertently left cattle in the bush and they were taken by lions or spotted hyenas (16%), and when approaching lions caused cattle to panic and break out of the boma despite the presence of herders. Success of those attempts varied widely, from 100 to 0%, depending largely on boma construction. Ranchers identified density, rather than height or thickness, of thorn bush walls as the most important factors in containing panicked cattle; bomas constructed of stone walls or surplus wooden posts with wire on top were uncommon but invulnerable to stampeding cattle, and thick well-maintained thorn bush were intermediate in efficacy. Flimsy bush bomas afforded poor protection. Because cattle usually broke out through "gates," a dense tree pulled into the opening, boma complexity was also reported as a factor: bomas with more "rooms" (separate compartments) had more internal gates, impeding panicked cattle from bursting out through the main gate. When lions were detected near bomas, they were chased off by shouting, banging pots and pans, or firing shotguns loaded with birdshot in the air; night guards were instructed not to shoot at predators. Some ranches used dogs to warn of predators, both at bomas and in the field, but others did not allow dogs because herders used them to hunt wildlife.

Management and lion predation on livestock

In the words of one ranch manager "If I lose livestock to predators it is my own fault," meaning that careful management would prevent nearly all predation on livestock. Two neighboring ranches illustrate the influence of husbandry on lion predation and retaliatory killing. Ranch One raised 2,100 cattle, kept in thorn bush bomas at night and 5,000 merino sheep, kept in flimsy portable wire bomas at night. In 1995 and 1996, lions killed 25 cattle and 201 sheep, and 19 lions were shot between 1995 and 2009.

Ranch Two bordered One and raised 2,300 cattle and 200 sheep and goats, also kept in very stout and well maintained thorn bush bomas. No stock were lost to lions in 1995–1996, and only two problem lions were shot following predation on cattle between 1995 and 2017.

Both ranchers agreed that the disparity was due to management. Sheep could not be kept in robust permanent bomas as they needed to be moved every few days to prevent disease and preserve wool quality, but the portable wire enclosures were particularly vulnerable to lions leaping in. Thorn bush bomas on Ranch One were not as stout or well-maintained as on Ranch Two, as it had relatively fewer trees and the owner was reluctant to cut them. Once it adopted "lion-proof" mobile bomas (below) and stopped raising sheep, predation losses declined markedly and only four persistent problem lions were shot between 2010–2017.

This comparison also illustrates the importance of stability in the lion population. A pride with a home range that included Ranch Two but not Ranch One rarely killed livestock and suffered almost no shooting mortality. One which ranged largely on Ranch One persistently took poorly protected stock and its members were regularly shot. Frequent turnover was thought to contribute to persistent livestock predation because the group as a whole did not learn that livestock were largely unavailable as prey. After management improved on Ranch One and livestock predation and lion shooting slowed, that pride subsequently also remained largely stable.

Costs of tolerating lions

Permitting predators to exist on the commercial ranches entails a variety of costs. Besides the market value of cattle killed by lions, expenses include the costs of employing herders, night guards, security personnel, building bomas, buying and maintaining vehicles, and minor equipment such as torches.

However, these costs come with a large *caveat*. Besides providing anti-predator vigilance, security personnel are focused on theft prevention and herders are responsible for driving herds to grazing and water, vigilance, and daily husbandry and health monitoring. Laikipia borders northern Kenya, where livestock raiding is still a way of life among young men; in the absence of herders, night guards at bomas, and security forces, ranches would be vulnerable to well-armed raiders; communally-owned

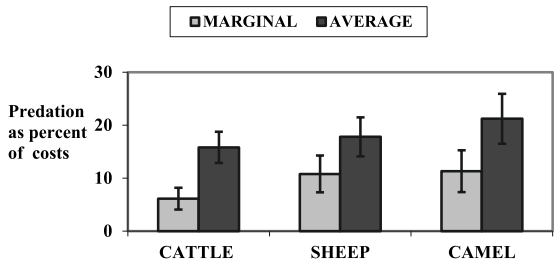

FIGURE 4
Predation as percent (+ SE) of annual costs of rearing livestock on twenty Laikipia commercial ranches in 1995–1996 (Marginal: F = 1.03; df = 2.40; p = 0.36. Average: F = 0.50; df = 2.40; p = 0.61).

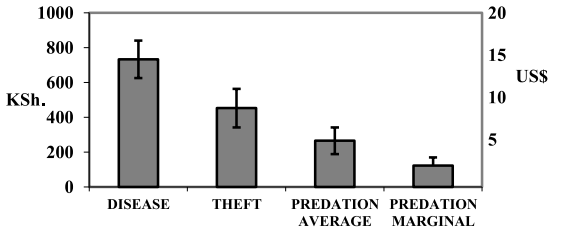

FIGURE 5
Annual cost in Kenya shillings and US dollars of disease, theft, and predation (+ SE) per head of cattle on twenty Laikipia commercial ranches in 1995–1996 (F = 8.75; df = 3.76; p = 0.00005).

group ranches regularly lose livestock in raids, which often also result in human fatalities. Ranchers were thus asked to apportion costs among the different predators, husbandry unrelated to anti-predator vigilance, theft prevention, and whether they could dispense with bomas and herders if there were no predators. They agreed almost unanimously that bomas would still be essential for managing livestock in this region. The one exception, which kept cattle in fenced paddocks 24 h/day, was in southern Laikipia, away from the frontier with northern Kenya and surrounded on all sides by commercial ranches or communal agricultural land, thus relatively protected from raiding.

Because of theft, ranchers also stated that in the absence of predators, they would not be able to reduce the number of security personnel, vehicles, or bomas, and that they could only reduce their herding staff by a mean of 3%. Thus, without large carnivores, herding and security costs would not change materially. We calculated *average* costs of predators as including all those allocated to the time herders and security personnel devoted to prevention of predation on livestock, as well as the value of stock killed or injured, while *marginal* costs were only those which would have been incurred in the absence of predators (**Figure 4**). That is the value of livestock killed by predators, which in Laikipia was a more realistic estimate of predator impact on ranch operating costs than average costs (for calculations, see **Supplementary material**).

Because ranches varied in area and number of cattle, cost of predation was also calculated on a per head basis, **Figure 5**. When controlling for all costs unrelated to predation losses and avoidance, for the mean ranch in Laikipia the marginal cost above that if there were no predators was $1.54 (1997 dollars) per head of cattle. Lions were responsible for 64% of predator costs, less than one dollar per cow, with spotted hyenas accounting for 26%, and leopards 10%, taking exclusively calves.

All ranchers interviewed emphasized that their estimates of lion numbers on their properties were rough guesses, and these yielded a density estimate of 5.6/100 km^2, which extrapolated to an estimated 175 in the county. They also thought that the population had been stable over the prior 5 years. Subsequent research showed that their population estimates were surprisingly accurate, and lion numbers in the study area did indeed remain stable for the duration of the study.

Based on each rancher's estimate of the number of lions on his property, and excluding one with extreme predation problems due to poor husbandry, it cost $226 to maintain one lion on a cattle ranch in 1996. Given that lions are the primary draw for tourists in Africa, that cost was minor compared to the value of lions on ranches with tourism operations.

Lethal control

Until The Wildlife Act of 2013, lions were classified as "vermin," and it was legal to kill any that killed or threatened livestock. From the outset, we made it clear that we understood the financial impact of predation and avoided seeming judgmental about shooting lions to protect livestock and livelihoods. Ranchers were open about predator control and none interviewed in 1997 appeared reluctant to report shooting lions or other predators. Of the 25 commercial ranches, 20 were active in or sympathetic to conservation and tourism, and interested in maintaining or increasing predator numbers. They saw predation losses as part of the cost of the livestock business, and all but one of those surveyed wanted to maintain or increase predator numbers, as long as impact on their business did not increase. Five ranch owners reported little interest in conservation. We were confident that the 20 conservation ranches subsequently reported lion shooting promptly and accurately, but from radio tracking we knew that all of the five ranches uninvolved in conservation shot lions and did not report to us. Thus, recorded mortality data represents minimum numbers.

Ranchers asserted that they were highly selective about removing persistent problem animals. None reported shooting lions on sight or using poison, which were standard practices in the past (Denney, 1972), nor killing lions the first time they took livestock, ignoring 67% of lion predation as a cost of doing business. When a group of lions consistently killed livestock, a rancher would "sit up" over a fresh cattle kill the following night and shoot one lion when the group returned to the carcass. Although males and females were reported to be equally likely to kill cattle, ranchers reported killing nearly twice as many males as females.

Early data showed highly variable rates of lion shooting among ranches, clearly related to livestock husbandry practices. The average ranch shot 1.75 lions annually in 1995 and 1996, but with wide variance, ranging from 0 to 19, the former often having no lions present while the latter, Ranch One above, raised sheep, which were particularly vulnerable to lions. The ranch which kept cattle in fenced paddocks rather than bomas overnight relied on strict predator control to protect cattle, shooting 12 in 1995–1996. With

that exception, nearly all ranchers expressed interest in maintaining lions and other predators on their lands; in 1997, they were either content with their current number or wanted to see an increase of, on average, 22%.

Sixty-three lions were known to have been shot on surveyed ranches in 1995 and 1996, plus another three reported by the Kenya Wildlife Service. More were no doubt shot on ranches which did not participate in the survey, but based on ranchers' lion population estimates, shooting of problem animals killed 20% of the population annually. Subsequent field data proved that the rancher estimate of lion numbers were accurate, as was the calculated mortality rate.

Data collected between 1998 and 2002, when lion numbers were well documented, recorded 19.6% annual mortality of adults and sub-adults (Woodroffe and Frank, 2005), remarkably close to the earlier estimate based on ranchers' estimates of lion numbers and reported shooting. That study also supported their assertion that they were accurate in identifying and removing known persistent stock killers, as lions initially collared at a cattle kill were 3.8 times more likely to be shot for subsequent predation than were collared lions with no known history of cattle killing. Twenty out of 21 shot lions we examined had either been shot at a livestock kill or had livestock remains in their stomach.

Further, females known to be stock raiders had lower reproductive success than those without a documented history of predation: cub survival among those born to mothers who were collared on livestock kills was only 37.5% that of cubs born to females collared under other circumstances. A simple Lewis matrix model suggested that the subpopulation of cattle-killing lions would decrease, while the number of lions that did not kill livestock would increase. Subsequent data have shown that the lion population has been stable since at least 2003 and, given the reduction in lion killing and low number of deaths due to natural causes, dispersal from the commercial ranches to communal lands, where few lions survive very long, is the most likely explanation for population stability on the ranches.

Mortality sinks

All Laikipia lions move over 3–6 ranches, and as a consequence, poor husbandry on an individual ranch which leads to a high rate of lion control can result in it becoming a mortality sink for a larger region. One such is described in Woodroffe and Frank (2005), Ranch One above. Frank (2011) describes another sink, the ranch which keeps its cattle in paddocks rather than using night time bomas, and did not tolerate wildlife which competes with cattle for grazing. It dealt with predation on livestock by shooting any lions suspected of threatening cattle. A pride known since 1998 had a home range centered on three ranches which had good cattle husbandry and minimal predation problems. Only 2.7% of all aerial fixes ($n = 300$) of the four collared females from this pride were on the paddocked property, yet 9 of the 10 pride members, including five breeding females, were shot there, eliminating the pride. As we only learn of deaths in collared prides, these represent an unknown fraction of the total killed on this single ranch. Thus, a minority of the 25 commercial ranches in Laikipia accounted for the majority of regional lion deaths. Even if a community of landowners wants to support predators, a few with poor husbandry and little interest in conservation can jeopardize the population of an entire region.

Boma study

To further elucidate the factors most important in limiting livestock predation losses, Ogada et al. (2003) studied livestock management practices on nine commercial ranches and one communal group ranch in 1999 and 2000. As had been reported earlier by ranchers (Frank, 1998), about 75% of losses to lions occurred when they raided bomas at night, usually by stampeding cattle, the remainder while livestock were grazing by day. Similar to the earlier analysis based on rancher descriptions of boma construction, no measure of boma factors (materials, height, thickness of walls) had a significant deterrent effect on livestock predation rates in this study. Counter to their experience, complexity (number of rooms) did not reduce losses. This unexpected result may have been due to short study duration during a severe drought, when lions took few livestock; only one was known to have been shot in this period.

Two other measures, however, were effective at reducing lion predation: the number of people living at each boma, and the presence of dogs. Larger numbers of people were associated with lower rates of lion predation on both cattle and shoats. Presence of dogs deterred loss of cattle but not shoats to lions, nor did they reduce predation by other carnivores. In a study of pastoralists' anti-predator measures on communal lands of Laikipia, Woodroffe et al. (2007a), found that the presence of dogs reduced day time losses by 67% and losses at bomas by 59%. Distance of bomas to cover did not significantly reduce rates of lion attacks on cattle. The factors most important in protecting ranch livestock at night reflected the system which had evolved among traditional pastoralists, with people and dogs living next to thorn bush bomas.

Because we did not have data on the total number of livestock herds out grazing every day, it was not possible to measure the number *not* attacked on any given day, so we instead looked at number of stock killed per daytime attack. However, during the study period, no lion attack on grazing cattle killed more than one animal, so analyses were restricted to small stock. Number of shoats lost per daytime lion attack was inversely proportional to the number of herders per herd. Although insufficient data precluded analysis, a higher ratio of herders to livestock almost certainly reduces the vulnerability of cattle, too.

Mobile bomas

A revolution in cattle husbandry occurred around 2004, with the development of "mobile bomas" by John Harris for sheep on Suyian Ranch and Giles Prettejohn for cattle on Ol Pejeta Conservancy. These comprise panels of chain link fencing supported by frames made of welded water pipe, which interlock to form a boma of any desired size and can be readily dismantled and moved (**Figure 6**). Cattle panicked by lions are unable to break out, nearly eliminating night time predation losses, and the design was so successful that it was rapidly adopted by most commercial ranches in Laikipia.

FIGURE 6
"Lion-proof" mobile boma developed by a Laikipia rancher, consisting of interlocking panels of steel pipe and chain link fencing which can be disassembled and moved to another location. These are strong enough to resist stampeding cattle panicked by lions and dramatically reduced night time livestock losses.

The mobile bomas also had unanticipated benefits for rangeland management and restoration:

(1) By moving them at intervals, grazing pressure can be spread more evenly over a property than when constrained by permanent bomas in fixed locations.
(2) They eliminate the need to cut trees and shrubs for boma construction and maintenance, a major benefit on conservation-oriented properties.
(3) When moved after a few weeks or months in one spot, the mobile bomas leave behind a thick layer of dung, which sprouts lush grass after rains commence. Parts of Laikipia are badly degraded from past overgrazing, and the mobile bomas have proved very useful in rehabilitating mineral soil to productive grassland. An area of degraded soil can be gradually restored by stepping bomas across it, simply leaving a few panels in place, while unfolding the circle formed by the other panels and moving them to form a new boma immediately adjacent to the prior site.

Disadvantages of this very effective design are the $2–3,000 cost and the need for a truck or tractor to move the panels to new sites. Given the durability, the savings in livestock losses, preservation of trees, and their function in restoring degraded soils, these costs are justifiable and within the reach of commercial ranches, which have trucks and tractors anyway. However, the costs of mobile bomas are too expensive for most pastoralists. A community could only afford them with financial help from government or an NGO, and maintenance would require a technician and vehicle. For expensive bomas to be economically feasible on community lands, livestock owners would probably need to gather their separate herds into a central boma at night. Pastoralists, however, indicated that such a change in traditional practice, by which each man has his own bomas in his own manyatta, would meet with considerable resistance and was not considered to be an acceptable alternative.

An unanticipated consequence of reduced nocturnal cattle predation on the commercial ranches was an increase in day time lion attacks while herds were grazing. In response, ranches modified their herding practices with incentives for herders to be vigilant, such as bonuses in cash or livestock if he lost no cattle to predators over a specified period.

Lion ecology

Capture

Field research on lion ecology commenced in 1998. Most of Laikipia is rugged semiarid bush country, punctuated by rocky

hills and escarpments, and many flat areas are strewn with lava rock and nearly inaccessible by vehicle. After a century of predator control, Laikipia lions were nocturnal, secretive, and rarely seen, so direct observation and following by vehicle were not feasible, and movement data could only be collected by radio collaring.

As few lions were approachable for free darting, early capture efforts employed large cage traps, but most lions are reluctant to enter them. Further, those that were caught sometimes damaged their claws and teeth attempting to escape; leopards were particularly likely to damage themselves (Frank et al., 2003). Foot snares developed for research on bears (Proulx, 1999) and later adapted for other New World carnivores appeared to be a promising technique, but commercially available Aldrich snares proved ineffective for capturing lions. In 2,000, professional trapper Dairen Simpson spent several months in Laikipia, adapting his own foot snare design and methodology for African lions (Frank et al., 2003). When lions were known to be in the vicinity, a livestock or wild ungulate carcass was tied to a tree, and the vehicle with loudspeakers stationed 2–300 m away, playing sounds of a distressed buffalo calf, hyenas on a kill, and lions confronting hyenas. When we heard a lion being snared, it was immobilized with medetomidine (0.03–0.04 mg/kg) and ketamine (2–3 mg/kg, concentrated to 200 mg/ml) for collaring. The medetomidine was reversed with atipamezole when the lion started to rouse, roughly 1 h after darting.

Lions were captured on 56% of attempts, and the snares caused no visible damage to lions or spotted hyenas, which were frequent by-catch. Other pride members would often remain nearby, but spotlights discouraged them from approaching while we collared, measured, and sampled the lion. In later years, as reduced persecution made lions more approachable by vehicle, we were increasingly able to use free darting. Between 1998 and 2015 we captured and recaptured 220 lions a total of 336 times.

Very high frequency collars

From 1998 until 2010, lions were fitted with very high frequency (VHF) collars (Telonics Inc., Sirtrack Inc., Mesa, AZ, United States and Lotek, Inc., Havelock North, New Zealand), located from aircraft roughly once per week in the early morning. We recorded group size and composition whenever they were visible in open areas. Maps generated from radio locations were sent to ranches by email after each flight. Early attempts to use 8 ARGOS and GPS-ARGOS collars were expensive disappointments, each collar soon failing, and each for a different reason (Frank, 2002).

Although the irregular location data may have been of limited value in avoiding livestock losses to lions, an unanticipated benefit of collaring was that ranchers started to take interest in their lions as individuals, often giving them names in addition to our ID codes. They reported that this familiarity made them more tolerant of cattle losses and reluctant to shoot named problem lions. Interestingly, we saw a similar response among Maasai pastoralists in the Amboseli region when the Lion Guardians were able to name and share information about collared lions with their communities (Dolrenry et al., 2016; Hazzah et al., 2017). Several Laikipia ranches bought VHF receivers and started tracking on their own, either purely out of interest, in order to avoid herding cattle near them, or sometimes to find lions for lodge visitors. Early in our research, a rancher who had shot a great many lions in his career spent so much time with collared groups that they became habituated to his vehicle within 1 year. He knew and named all lions on his ranch, collared or not, and on the rare occasions that one became a chronic stock killer, was able to selectively remove the offender. Other ranches, particularly those with tourism, took similar interest in their lions and this familiarity, along with improved management and decrease in predation losses, appeared to be a significant factor in the reduction of retaliatory shooting.

Collars also led to the discovery of several lions which had been shot and not reported to us, as well as 22 dead lions which had moved onto adjacent community lands from the relatively safe ranches at night, taken livestock, and were then poisoned in retaliation. Pastoralists poisoned lions and hyenas with the cheap and ubiquitous agricultural insecticide carbofuran, sold by an American company under the trade name Furadan (Frank et al., 2011), which is highly toxic to birds and mammals. Poisoning decreased significantly after the manufacturer of Furadan withdrew it from the East African market following an exposé in the influential American TV news program 60 min. However, other readily available pesticides are now used more often, and Kenya did not ban the importation of generic carbofuran from Asia.

Lion density

Three different methods of estimating lion density showed that the educated guesses of ranchers recorded in the initial 1997 survey (Frank, 1998) were surprisingly accurate.

(1) On several morning tracking flights in 2003, all collared groups on eight properties amounting to 1,493 km^2 were found in the open, allowing for accurate counts. Extrapolating from those minimum numbers, we estimated a county-wide lion population of about 218 adults and subadults, a density of 6.5/km^2.

(2) In 2005, Thomas Stephens ran spoor transects (Stander, 1998) on three ranches on which all lions were known (Stephens, T. unpubl., BSc thesis, University of Southampton). The calculated density of 6.15 adult and subadult lions per 100 km^2 accurately reflected true density of individually known lions on those properties, and was extrapolated to an estimated total population of 231 $\pm$ 50.5 for the wildlife friendly area of Laikipia County.

(3) In 2011–2014, Marcelino Napao Iruata identified (Pennycuick and Rudnai, 1970) all lions in 12 contiguous groups in a study area of 1,322 km^2, calculated from the cumulative range of all groups as determined by Global positioning system (GPS) collars. A snap shot of numbers in 2014 showed a population of 103 known individuals in the study area, for a density of 7.8 individuals of all ages per 100 km^2. Excluding cubs, the estimated density was 5.8/km^2 (Iruata, 2016).

Thus, density estimates derived from three different methods over the 12 year period of 2003–2014 were in close agreement, ranging between 5.8 and 6.5 adults and subadults per 100 km^2, reflecting stability of the population, as was asserted by ranchers in 1997.

Group size

The mean number of adult females in the twelve monitored groups was 2.4, with a mode of two. Although one group had 6

adult females, the modal size of two may have been a reflection of persecution. Prides were larger in northern Laikipia, where by 2010 all ranches had adopted mobile bomas and avoided shooting lions, and smaller in central Laikipia, where four ranches had poor livestock practices and still regularly shot lions. All groups in this area ranged over at least one of those properties. The mean male coalition was 2.0 individuals, and the largest group of dispersing young males was six.

Home range size

Pride home range sizes were calculated from 21 VHF-collared females and 18 males with >30 fixes obtained in early morning at least 1 week apart between 1998–2009, and 10 female and four male GPS collared lions between 2006–2011, programmed to take hourly fixes between 1,800 and 0700, plus one at 1,200. Minimum convex polygons were created in ArcMap 10.2 (ESRI, Redlands, California), **Table 1**. The larger ranges revealed by GPS collars were a reflection of nocturnal movements, often into communal lands where lions were rarely found in morning VHF aerial tracking.

Predation on wild prey

O'Brien et al. (2018) studied predation ecology by collaring 21 females with GPS Iridium collars (Vectronic Aerospace, Berlin, Germany) set to take hourly fixes between 1800–0700 h and to upload data at 0700 daily. Inspection of all clusters of three or more fixes (indicating a stay of >2 h) the next morning identified 768 kill sites; as there were spotted hyena tracks at many of these, a small proportion may have been killed by hyenas and scavenged by lions. Common zebra (*Equus quagga*) constituted 44.3% of kills, cattle 12.6%, eland (*Taurotragus oryx)* 8.5%, reticulated giraffe (*Giraffa camelopardalis reticulata)* 5.2%, with another 24.7% divided among other common wild herbivores and the remainder a miscellany of less common species. Shoats constituted 1.2% and elephant calves 0.5% of kills.

Grevy's zebra

A primary motivation of the predation study was to assess lion impact on the highly endangered Grevy's zebra (*Equus grevyi*), which was once widespread in northern Kenya and the Horn of Africa but has been extirpated from most of its former range. Today Laikipia is home to over 50% of the estimated 2,350 remaining in Kenya. To investigate whether lions preferentially hunted Grevy's zebra, as had been suggested on a fenced reserve (Rubenstein, 2010), O'Brien et al. (2018) used random gas models incorporating GPS collar movement data from lions, Grevy's and common zebra, the predation data, and density estimates of both zebras from line transect counts. They found that Grevy's were taken less often than predicted, while common zebra were taken as or less often than predicted. As the recruitment rate of Grevy's in Laikipia had tripled since 2004, they concluded that lions were not a significant threat, and that the primary impacts on Grevy's were displacement from grazing by cattle and competition for grass with common zebra, which outnumber Grevy's in Laikipia by a factor of 22 to 1.

Movements and avoidance of human activity

Several studies have looked at space use by Laikipia lions in relation to daily human activity patterns. Oriol-Cotterill et al. (2015a) deployed GPS collars (Vectronic Aerospace GPS Plus) on five female lions, set to take a fix every hour through the night and one at noon. Data were downloaded periodically via ultra high frequency (UHF) link. As in earlier studies using VHF collars and morning aerial tracking, lions were found to prefer commercial ranch lands over pastoralist areas, which had higher densities of both livestock and people, lower tolerance of lions, and less wildlife. However, GPS data showed that lions use pastoralist areas more than was evident in the earlier study, mostly at night when humans and livestock are in manyattas, and return to safer commercial ranches by day. Lions moved faster on pastoral areas, particularly in the dry season, and changed direction less often.

A key finding was that lions also tend to move closer to bomas on commercial ranches at night when human activity is low, cattle are vulnerable to being stampeded, and strays might be found nearby. They came closer to bomas on nights with less moonlight and during rainy periods. They also tended to use daytime rest sites closer to bomas during the rains than in the dry season. They tended to speed up and maintain direction of travel as they approached bomas, and moved away more slowly, perhaps staying in the vicinity due to presence of wild prey or the possibility of finding stray livestock. Ranchers and herders had reported that zebras and other grazers move toward bomas at night, speculating that they are avoiding lions which in turn are avoiding human presence. However, these results suggest that lions may in fact be attracted to boma sites by the presence of both livestock and wild prey.

Thus, rather than totally avoiding the areas around bomas where human activity and disturbance is high, lions partition their foraging by utilizing these potentially prey-rich but dangerous areas at night and moving away by day. Oriol-Cotterill et al. (2015b) term this pattern of habitat use a Landscape of Coexistence, a subset of the Landscape of Fear (Laundre et al., 2010), by which animals threatened by humans are able to utilize resources more fully by

TABLE 1 Lion home ranges on commercial ranches in northern and central Laikipia County, as obtained through very high frequency (VHF) collar fixes on morning tracking flights, and Global positioning system (GPS) collars set to take one fix per hour through the night.

Sex	VHF 100% MCP (km^2)	VHF 95% MCP (km^2)	100% GPS MCP (km^2)	GPS 95% MCP (km^2)	VHF 50% core area (km^2)	GPS 50% core area (km^2)
Female	282.2 ± 39.1	175.9 ± 25.9	388.7 ± 82.5	262.3 ± 54.4	49.9 ± 6.4	80.3 ± 26.8
Male	456.2 ± 68.76	328.2 ± 66.9	508.1 ± 165.9	355.7 ± 129.8	71.31 ± 14.2	52.9 ± 11.8

From Iruata (2016).

adapting their behavior temporally to anthropogenic risk rather than entirely avoiding human-dominated landscapes and the prey therein.

Subsequent work with more sophisticated GPS collars equipped with accelerometers yielded much more fine grained data and refined earlier conclusions (Suraci et al., 2019). Nine females and five males from different prides were fitted with SMART (species movement, acceleration, and radio tracking) collars (Wilmers et al., 2015) which took fixes every 5 min and recorded continuous acceleration data in three dimensions. These data were converted into overall dynamic body acceleration (ODBA) and an algorithm to identify behavior was developed, based on ODBA, step length (distance between consecutive locations) and turning angle between steps. The algorithm identified five behavioral states from the acceleration data: feeding, active resting, inactive resting (sleep), traveling in long relatively straight steps, and meandering in short steps with greater turning angles and brief bursts of acceleration. Feeding was characterized by frequent high acceleration, indicating rapid head movements.

Suraci et al. (2019) showed that although lions were indeed avoiding bomas by day, tending to stay over 2 km away regardless of habitat type, they showed a strong tendency to feed within 1 km of bomas at night, particularly when there was cover nearby; they avoided feeding near bomas in open habitat. Between 18–22% of time spent feeding at night was within 1 km of a boma, but feeding events fell off rapidly as distance to a boma increased. When inactive by day and thus more vulnerable to being detected by humans, they avoided bomas, when people are active in the vicinity. As 87% of investigated kill sites within 1.5 km of bomas involved wild ungulates rather than livestock, it seems likely that lions were attracted to boma sites by availability of natural prey rather than opportunities to take livestock. Analysis of movements in relation to nocturnal lion feeding sites before and after a boma was erected showed no preference until the boma was in place; the presence of livestock and humans seems to be a attractant even though livestock were taken there infrequently. These findings support herders' reports of frequent nocturnal wildlife kills within earshot of their huts. While it is likely that ranchers site bomas in areas of good grazing for both cattle and wild ungulates, probably at a finer temporal scale since the adoption of easily moved mobile bomas, wild grazers also avoid areas of human activity around bomas by day but utilize them at night. Thus, bomas attract wildlife at night, and the lions follow.

Nisi et al. (2022) used the same dataset to look at lion response to topography and bomas, comparing movement patterns to pumas (*Felis concolor*) in mountainous terrain with scattered human dwellings in central California. On short (5–15 min) timescales, African lions of both sexes tended to avoid steep slopes and moved more slowly on them, but on timescales over 1 h, only males avoided steeper slopes while females did not, suggesting that females tend to drive longer movement patterns. Reflecting Suraci et al. (2019), both sexes tended to move closer to bomas by night while avoiding them by day, and to move faster when in the vicinity of bomas, as Oriol-Cotterill et al. (2015a) found using coarser movement data (fixes on 1 h intervals).

Nisi et al. (2022), interpreted these results in terms of energy expenditure in relation to risk of anthropogenic mortality. Slower movement in steep terrain conserves energy, and male avoidance of it may reflect their longer movements and larger home range in patrolling territories. However, the fact that lions relax their avoidance of humans at night in order to exploit prey availability near bomas shows that they balance the trade-off between feeding and risk by apportioning habitat use temporally.

These studies demonstrate that behavioral flexibility is a key to lion persistence on livestock rangelands. That lions use boma areas at night may in part reflect foraging for opportunities to take livestock, but areas around bomas are also attractive to wild grazers at night, even though they also avoid bomas by day. Prey and predators both utilize them when human disturbance is minimal, accessing resources that would be unavailable were avoidance of humans absolute.

Global positioning system early warning system

The real time GPS collars in the predation study afforded an opportunity to inform ranchers of lion day time resting sites. Each morning we emailed participating ranches a map of 7 a.m. fixes, allowing managers to direct herders away from lions, significantly reducing day time kills. This system was further refined and expanded in 2015 when Chris Wilmers and Terrie Williams of the University of California, Santa Cruz, joined us to study lion ecological energetics. The Wilmers lab created a website, Africanlion.org, which automated the mapping, allowing ranch managers to check 7 a.m. sites without the need for emailed maps.

Lion rescues

Real time collars also directly saved four lions' lives and revealed illegal killings. In 2014–2016, real time movement data led us to:

- Three lions shot illegally;
- Two starving lions caught in snares;
- Two starving lions trapped inside a newly fenced area (**Figure 7**).

The trapped lions all survived because the collars alerted us to their situation and we were able to immobilize and free them. Similar rescues are unlikely in the future, as today only veterinarians are allowed to immobilize wildlife and are rarely available on short notice.

Although highly effective for avoiding lion attacks on cattle, our use of GPS collars transmitting near real time data was only possible because they were purchased for research. At a cost of US$ 3–4,000, use in a large area is probably not financially feasible in the absence of such funding. Moreover, batteries need to be replaced at intervals, requiring expensive and time-consuming capture of each study animal.

Decreasing anthropogenic mortality over time

Between 1998 and 2016, we recorded 337 lion deaths in Laikipia, of which 202 were known and monitored animals.

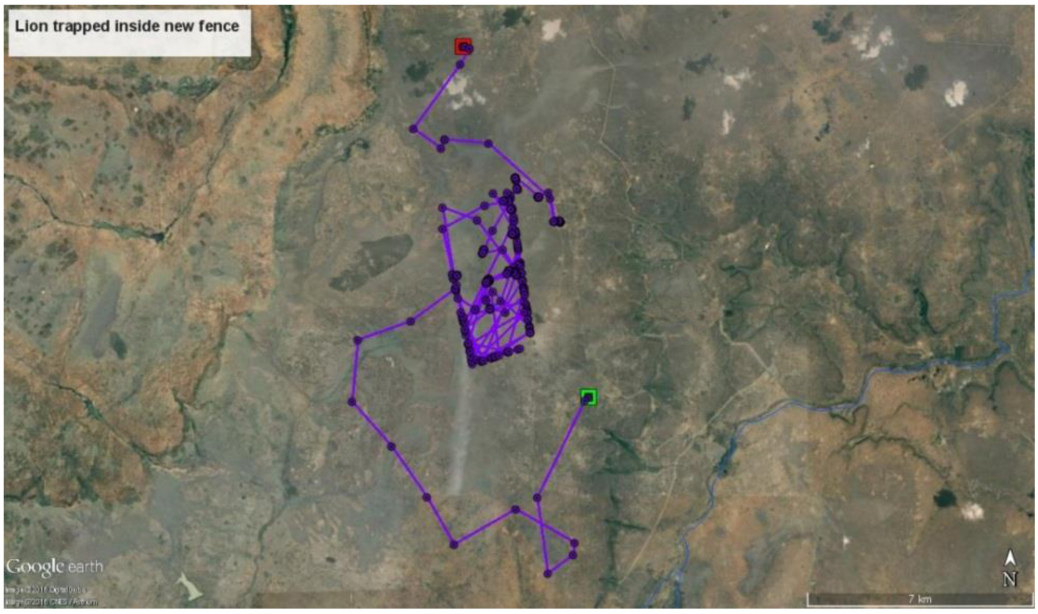

FIGURE 7
Global positioning system (GPS) collar data from a male lion trapped inside a newly constructed fence. When he was seen to be moving in a rectangle, he was immobilized and released outside the fence. He had lost 50 kg while trapped.

Among known animals for which cause could be determined, anthropogenic deaths accounted for 88% and 12% were of natural causes. We also recorded 125 deaths of previously unknown lions, most of which were reported by others, and 93.6% of those were anthropogenic. The slight difference in anthropogenic deaths between known and unknown lions is not significant but in both cases natural deaths were less likely to be detected and reported.

Mobile bomas, more vigilant herding, and the GPS collar early warning system reduced livestock losses. Along with ranchers' increasing reluctance to kill problem lions, these improvements led to a 90% reduction in lions shot in retaliation for livestock predation on the commercial ranches between 2001 and 2017, **Figure 8**.

Uniform regional livestock management

Although most commercial ranches are committed to wildlife and habitat conservation, several in central Laikipia are not. They do not have tourism, the rangeland is overgrazed, bomas are poorly maintained, and they also shoot more lions than other properties. Presumably due to higher mortality, females in this area form smaller groups than in northern and eastern Laikipia, where ranches uniformly practice better livestock management. We believe that the more vulnerable cattle and higher rates of predation on these ranches help maintain the stock-killing habit in lions that range over them, thereby also exacerbating lion problems on neighboring ranches with better management.

The influence of effective cattle protection was starkly illustrated in 2016, when heavily armed pastoralists invaded Laikipia from the north and west, bringing 230–250,000 cattle and over 350,000 shoats to graze on the commercial ranches and small farms (Hetz, 2017; Masiaine et al., 2021). The invaders were pushed south onto the well-managed rangelands of Laikipia by lack of grass on their severely overgrazed lands, encouraged and abetted by local politicians of their tribes in an election year. Laikipia residents were killed, lodges and homes looted and burned, and the land was quickly grazed bare, the lack of forage displacing wild grazers. Wildlife, including lions, were killed. The pastoralists constructed flimsy temporary thorn bush bomas and with the reduction of wild prey, lions which formerly had not preyed on livestock started taking vulnerable cattle. By the time the Kenya government encouraged the invaders to leave over 1 year later, many lions had resumed the cattle killing habit and losses of ranch cattle increased dramatically; unfortunately, data on the severity of losses were not available.

This event underscored the importance of regionally uniform livestock management practices. Lions seem to gradually lose the habit of taking livestock when prevented by strong bomas and vigilant herding. But because they range widely, moving over several ranches, the habit is maintained if they are able to kill livestock on some properties with poor management, and lions thus continue to be a greater threat on well-managed properties within their home range.

Lethal control

In spite of protective measures, some lions may still become persistent problem animals and take more livestock than owners will tolerate. In such circumstances, it may be counterproductive for conservationists to resist removing the offender, as pastoralists will eventually take action, often by poisoning, rather than endure repeated losses; the lion and scavengers will die anyway and the community will become skeptical of conservation efforts. Based

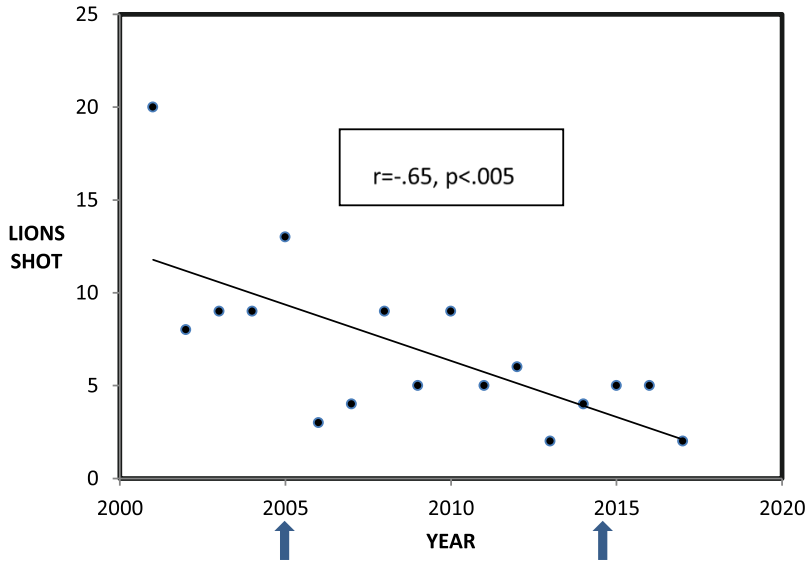

FIGURE 8
Decline in retaliatory lion shooting on commercial ranches of Laikipia between 2001 and 2017. Arrows indicate the introduction of steel and chain link mobile bomas in 2005 and the GPS Early Warning System in 2014.

on selective control as was practiced by ranchers in Laikipia (Woodroffe and Frank, 2005), Frank (2018) recommends a series of measures and decisions to guide policy on lethal control of persistent problem lions. Note that translocation is not considered a viable option because, unless habitat without resident lions or vulnerable livestock is available, translocated animals are unlikely to be tolerated by resident lions, mortality is high, and they continue to kill livestock as they try to return to their original home range.

Ideally, a program to minimize livestock predation should be in place, and livestock owners encouraged to adopt effective management practices to avoid predation. Only when those fail and a lion becomes a persistent stock killer should lethal control be considered. Criteria for removal may differ according to local circumstances; in an area with high densities of people and livestock but little wild prey, a decision to remove a lion might be made after fewer predation incidents than a similar lion where there is plentiful wild prey and tourism provides local economic benefits. All livestock predation incidents should be investigated by a trained team to determine whether livestock was actually killed by predators rather than scavenged after a disease or drought death, whether the owner managed his stock to minimize predation losses, and to accurately determine the species of predator responsible (Maclennan et al., 2009). Only when these conditions have been met should a persistent problem lion be humanely removed, and then only by a well-trained and well-equipped marksman.

Pastoralists, lions, and hyena proof bomas

Nearly all commercial ranches adjoin communally owned pastoralist lands, which sustain little wildlife but large numbers of people and livestock, mostly shoats. During the study period, one group ranch initially tolerated resident lions because it had a lucrative tourism operation but those were eventually poisoned. Group ranches without lions did sustain losses at night, however, but lions returned to the safer commercial ranches by day: only 1.5% of 3,658 morning aerial VHF fixes of 136 lions were on communal lands, and 42.6% of those were of three lions collared on the one tolerant group ranch. Subsequent GPS tracking of five female lions showed 13% of fixes on pastoralist land (Oriol-Cotterill et al., 2015b), mostly at night. Thus, lions spent most of their time on the relatively safe commercial ranches with abundant wildlife and returned to them after nocturnal forays into more dangerous and wildlife-poor communal lands.

Although lions were a problem for Laikipia pastoralists when they moved from commercial ranches onto communal lands and took livestock, spotted hyena predation on sheep and goats from bomas at night was more serious. This led to poisoning which also killed lions and scavengers; as a result, vulture populations have declined drastically in Kenya and one species is extinct (Ogada et al., 2016). Two factors made pastoralist livestock vulnerable: flimsy thorn bush bomas in which the "gate" was a tattered bush pulled into the opening at night and readily penetrated by hyenas, and the custom of throwing food and livestock remnants outside dwellings, which attracted hyenas to settlements. Bomas were poor because the larger trees had been cut, leaving only small shrubs which were unsuitable for building dense walls.

Steven Ekwanga developed inexpensive and simple modifications to prevent hyena incursions by surrounding the thorn bush wall with light livestock netting and replacing the bush gate with a solid one made from a sheet of corrugated iron or a 200 liter drum cut open and flattened (**Figure 9**). These modifications cost about the value of one goat.

With film makers Jenny Sharman and Richard Jones, Ekwanga made videos in both Swahili and Maa, the local language, which detail the construction of the modified bomas, herding practices, and the role of large carnivores in local lore and

FIGURE 9
"Hyena-proof" modification to a light thorn bush boma on a Laikipia pastoralist group ranch. The bush is surrounded by livestock netting laid on the branches and pegged to the ground, and the bush gate replaced with a sheet of corrugated iron or flattened 200 liter drum.

tradition. Ekwanga held over 200 *barazas*, open air meetings, all over Laikipia and Samburu Counties, at which he showed the video and demonstrated the boma modifications. Pastoralists reported that the modifications were nearly 100% effective in preventing hyena predation and, although we don't have data on uptake rates, these modifications are now widely used in both counties.

Associated projects

The original Laikipia Predator Project was one of the first studies to address the conservation and ecology of a lion population in unprotected livestock rangelands. It gave rise to several other large carnivore conservation and research projects in Kenya, the ones focused on lions under the umbrella organization Living With Lions.

- Aaron Wagner undertook a seminal study of striped hyena behavioral ecology in NE Laikipia (Wagner et al., 2007a,b, 2008).
- Rosie Woodroffe undertook a major study of wild dog (*Lycaon pictus)* ecology and conservation when they recolonized Laikipia after 30 years absence (Woodroffe et al., 2007a,b, 2012; Woodroffe, 2011a,b).
- Seamus Maclennan, Leela Hazzah, and Stephanie Dolrenry established the Kilimanjaro Lion Project on the Maasai pastoralist group ranches adjoining Amboseli National Park, where a recent upsurge in spearing and poisoning had decimated the lion population (Frank et al., 2006; Maclennan et al., 2009; Dolrenry et al., 2014, 2016, 2020; Hazzah et al., 2017). Their research included monitoring of a heavily persecuted, low density lion population and sociological studies on the changing relationships between traditional Maasai and lions. The latter gave rise to the highly successful Lion Guardian project, which employs young warriors to assist their communities in avoiding livestock predation and as effective field technicians, able to collect lion ecological data on a wide geographic scale which was not feasible using standard methods.
- Sara Blackburn studied lion numbers, distribution, and conservation on the communally owned conservancies north of the Maasai Mara National Reserve (Blackburn et al., 2016).

Discussion

As predators on large herbivores, large livestock-eating predators are among the most difficult animals to conserve; most of the world has dealt with the problem by simply eliminating them. Africa was the exception until the 20th century, when lion numbers and distribution were drastically reduced, first by indiscriminate predator control and sport hunting, and later by burgeoning human and livestock numbers. Much of the reduction

is ultimately attributable to habitat loss from expanding agriculture, habitat degradation from livestock overgrazing, and consequent disappearance of wild prey. The most important proximate cause has been direct killing in retribution for livestock predation. Even with a substantial base of natural prey, lions and other predators still take livestock at least occasionally, and are killed in retaliation. In some cases, cultural change from modernization and the growth of a market economy has diminished former tolerance of lions (Hazzah et al., 2009, 2014), leading to rapid loss or local extinction. Early reports of dense lion populations in Maasailand at the turn of the 20th century (Herne, 1999) gave way to decimation in the 1990's (Frank et al., 2006; Hazzah et al., 2009, 2017; Maclennan et al., 2009). Fifty years ago, lions were common even in the extremely arid region of today's Sibiloi National Park in northern Kenya (Thesiger, 1994) but are now absent due to reduction of wild prey and ubiquitous automatic weapons among local people (Willnerd, 2018; Torrents-Ticó et al., 2021).

The privately-owned commercial livestock ranches of Laikipia are a unique exception, not only in tolerating, but actively encouraging a stable population of lions among their livestock, going to considerable expense to avoid killing predators by investing in modifications of traditional African management methods. As an example of their attitude toward conservation, contrast Laikipia ranchers to those of the western US: wolves (*Canis lupus*) were reintroduced to the northern Rocky Mountains in 1995 against the vehement opposition of the politically powerful livestock industry. In 2005, the entire 71,600 km2 Yellowstone ecosystem lost 13 cattle and 71 sheep to wolves (Defenders of Wildlife, 2006), but in spite of monetary compensation for lost livestock and prompt removal of the offending wolves, the great majority of U.S. ranchers are still intensely opposed to wolf recovery: in 2021, the Idaho legislature voted to reduce the recovered wolf population by 90% (National Geographic, 2021). In 1995–1996, the average ranch in Laikipia, 0.18% the size of the Yellowstone region, lost 10.6 cattle and 52.3 sheep to predators (Frank, 1998); in 2017, two lions were known to have been shot on the ranches. Laikipia ranchers are not compensated for their losses, yet support a stable lion density of roughly 6/100 km^2, and robust numbers of Africa's other large carnivores. Beef production is not profitable, yet they accept costs of livestock protection and losses as a part of doing business.

Laikipia is obviously not a model for most of Africa, where livestock are kept by small farmers or pastoralists who lack the financial resources to invest in expensive mobile bomas and do not benefit from tourism income associated with lions. It does, however, demonstrate the practical feasibility of living with lions in livestock rangelands if local people have the will and resources, and has served as a laboratory for developing improved means of coexistence between humans and large carnivores.

"Lion-proof" bomas were the single most important development in reducing human-lion conflict on the commercial ranches, and reduction in night time losses more than compensated for increased day time predation. Further, incentives to improve herder vigilance reduced day time losses, and development of a GPS Early Warning System reduced them to negligible levels. Mobile bomas fabricated from steel frames and chain link fencing are too expensive to be purchased by most individual pastoralists, and, at least in Kenya today, long-established tradition may impede adoption of more cost effective communal use of fewer, centrally located mobile bomas shared by several families. The expense, effort, and continuing commitment required by more effective livestock protection measures contrasts to the low cost, low effort, and permanence of simply poisoning predators.

Although steel and chain link mobile bomas may not be economically realistic for most pastoralists, the living wall bomas made of chain link and fast-growing *Commiphora* trees developed by Lichtenfeld and her colleagues in northern Tanzania are also virtually 100% effective in protecting livestock from lions and hyenas, and at much lower cost (Lichtenfeld et al., 2015). Even without the living walls, reduction in losses to predators made plain chain link bomas cost effective within 2–3 years (Kissui et al., 2019). Although they do not have the same advantages of mobility, once established these require little maintenance and do not contribute to loss of woody vegetation, one of the main disadvantages of traditional thornbush bomas.

Current GPS collar technology and monitoring are expensive for use on a broad scale, and those used in Laikipia were paid for with research rather than conservation funding. In our experience, less expensive GPS collars have thus far been generally less reliable than costlier ones; given the amount of effort that goes into capturing secretive lions in unprotected rangelands, we found that the additional expense is more than justified by greater reliability. A more sophisticated, fully automated approach using geofencing technology and automated mobile phone SMS communications has been developed by Andrew Stein and his colleagues in Botswana (Weise et al., 2019). GPS collars and monitoring are affordable only by well-funded conservation efforts, and even then only on a limited scale, probably not realistic for lion conservation on the scale of large landscapes. The cost and effort may be justifiable for smaller scale conservation of lions in some pastoralist areas, however, perhaps just as a stop gap measure to prevent local extinction in the hope that changes in land use or economic priorities reduce human pressures on large carnivores.

The economic and cultural contrast between Laikipia ranchers and Maasai pastoralists illustrate the central importance of stakeholder involvement in conservation. Lions are of cultural importance to both groups as symbols of strength, power, and beauty, but they represent different costs and benefits to both groups. Losing a cow out of his herd of a dozen has greater economic and emotional impact on a pastoralist than the loss of a cow out of a herd of one thousand to a commercial operation (although the rancher who accepts the loss of a steer with reluctant regret may be considerably less philosophical about the loss of a valuable stud bull).

Many Laikipia ranches now include small, upscale tourist lodges to supplement cattle income, and the Mara and Amboseli regions of Kenya's Maasailand, are internationally famous for their wildlife, earning a large proportion of Kenya's roughly $1.5 billion tourism income (Kramer, 2022). Lions are the single most important attractions in both areas, but benefit landowners quite differently. Cattle production is not profitable, so tourism dollars spent in Laikipia are an important source of revenue for the Laikipia ranches. In Maasailand, however, little tourism profit reaches the individual pastoralists whose livelihoods are impacted by lion predation. Rather, money stays with the tourism operators, local and national government, and influential local elites who sequester income rather than distributing it equitably

to the communities and individuals who bear the cost of losing livestock to predators (Homewood et al., 2012). Thus, lions are a net economic positive on Laikipia conservation properties, but a significant negative to most pastoralists living near the lucrative lodges of Maasailand. Not surprisingly, even pastoralists in wildlife tourism areas have little to gain from tolerating predators; those in remote areas where tourists rarely venture have none. A major reason for the success of the Mara conservancies is that individual land ownership ensures that cattle owners benefit from tourism income, and for the success of the Lion Guardians on the communally owned group ranches of the Amboseli region is that many otherwise unemployable young men earn money and prestige from protecting both lions and their own communities.

Improvements in livestock protection and subsequent reduction in retaliatory lion killing are key to restoring and maintaining viable lion populations outside of parks and managed hunting concessions. Conservation projects throughout remaining lion range are developing new and effective measures, both technological and sociological, for alleviating lion-human conflict. Realistically, however, costs of these in pastoralist landscapes will probably need to be covered by NGO's, tourism enterprises, or governments for the foreseeable future. However, with cheap and effective poisons readily available, the additional effort required by conservation measures, even if paid for and facilitated by outsiders, are not likely to be embraced by rural people unless they perceive lions as improving their lives and economic welfare more effectively than the simple expedient of eliminating predators. Because most protected areas are too small, maintaining lions in surrounding pastoralist landscapes will be critical if wild lions are to survive in Africa.

Author contributions

LGF established the Living With Lions projects in Kenya, initially in Laikipia and later in the Amboseli and Mara regions, oversaw the work, and organized collaborators to undertake additional research.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1141195/full#supplementary-material

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