



Efficacy of Two Lion Conservation Programs in Maasailand, Kenya

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Abstract: *Lion (Panthera leo) populations are in decline throughout most of Africa. The problem is particularly acute in southern Kenya, where Maasai pastoralists have been spearing and poisoning lions at a rate that will ensure near term local extinction. We investigated 2 approaches for improving local tolerance of lions: compensation payments for livestock lost to predators and Lion Guardians, which draws on local cultural values and knowledge to mitigate livestock-carnivore conflict and monitor carnivores. To gauge the overall influence of conservation intervention, we combined both programs into a single conservation treatment variable. Using 8 years of lion killing data, we applied Manski's partial identification approach with bounded assumptions to investigate the effect of conservation treatment on lion killing in 4 contiguous areas. In 3 of the areas, conservation treatment was positively associated with a reduction in lion killing. We then applied a generalized linear model to assess the relative efficacy of the 2 interventions. The model estimated that compensation resulted in an 87–91% drop in the number of lions killed, whereas Lion Guardians (operating in combination with compensation and alone) resulted in a 99% drop in lion killing.*

Keywords: carnivore, community involvement, community-based conservation, conservation, compensation, conservation evaluation, incentives, local knowledge, tolerance

Eficacia de Dos Programas de Conservación de Leones en Maasailand, Kenia

Resumen: *Las poblaciones de león (Panthera leo) están disminuyendo en casi toda África. El problema es particularmente mayor en el sur de Kenia, donde los pastores Maasai han estado matando con lanzas y envenenando leones a un paso que asegurará una extinción local a corto plazo. Investigamos dos acercamientos para mejorar la tolerancia local hacia los leones: pagos de compensación por la pérdida de ganado por depredadores y Leones Guardianes, que parte de los valores culturales y el conocimiento local para mitigar el conflicto ganado-carnívoro y monitorear a los carnívoros. Para medir la influencia total de la intervención de la conservación, combinamos ambos programas en una variable única de tratamiento de conservación. Usamos datos de ocho años sobre la matanza de leones para aplicar el acercamiento de identificación parcial de Manski con suposiciones unidas para investigar el efecto del tratamiento de la conservación en la matanza de leones en cuatro áreas contiguas. En tres de las áreas, el tratamiento de conservación fue asociado positivamente con una reducción en la matanza. Aplicamos entonces un modelo lineal generalizado para*

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Paper submitted December 10, 2012; revised manuscript accepted October 6, 2013.

estudiar la eficacia relativa de las dos intervenciones. El modelo estimó que la compensación resultó en una baja de 87-91% en el número de leones matados, mientras que Leones Guardianes (operando en combinación con la compensación y solo) resultó en una baja de 99% en la matanza de leones.

Palabras Clave: compensación, conocimiento local, conservación basada en la comunidad, conservación de carnívoros, evaluación de la conservación, incentivos, participación de la comunidad, tolerancia

Introduction

Retaliatory killing of large carnivores by humans is a significant cause of carnivore population declines (Nowell & Jackson 1996; Woodroffe & Ginsberg 1998). African lion (*Panthera leo*) populations have declined drastically in the last 60 years; only an estimated 32,000 remain (Riggio et al. 2013). The decline is largely due to indiscriminate killing of lions by local communities that perceive little benefit from tolerating lions. The cost-benefit distributions of human-lion coexistence are skewed. Government, elected officials, and local tour and hunting operators gain economic value from lions, while local communities absorb the costs in livestock losses (Hemson et al. 2009). This inequitable incentive structure exacerbates indiscriminate lion killing (Dickman et al. 2011).

Various incentive-based strategies have attempted to improve attitudes and behavior toward large carnivores by distributing the benefits of carnivore presence more equitably. Mishra et al. (2003) found income generation from handicrafts helped curtail retaliatory killing of snow leopards (*Uncia uncia*) in Nepal, and Marker et al. (2003) showed that marketing predator-friendly meat could promote cheetah conservation on Namibian farmland. There have been limited attempts to emphasize the link between tourism and trophy hunting benefits and lion presence (Frost & Bond 2008), but few studies have documented the efficacy of incentive-based conservation efforts in reducing direct threats to carnivore populations (but see Jones & Weaver 2009).

Lions living in pastoralist areas of East Africa are speared to reinforce the role of warriors in society and are poisoned or speared in response to livestock depredation and as a symbolic act of protest against conservation restrictions (Kissui 2008; Hazzah et al. 2009; Goldman et al. 2013). Warriors (*ilmurran*) in Maasai society value bravery and respect and are responsible for defending their community and livestock from cattle raiders and wildlife.

Southern Kenya's Amboseli ecosystem, located in the center of Maasailand, provides a unique situation, where 2 incentive-oriented programs run simultaneously in an area with baseline historical data on lion killing. The Predator Compensation Fund (PCF) is based on the model of paying local people for depredated livestock in an attempt to deter retaliatory killing (Verdade & Campos 2004; Agarwala et al. 2010; Boitani et al. 2010). The

PCF program is a carefully designed compensation program with a complex system of incident verification, payments, and penalties for violating program rules. Lion killing by one individual can cause cessation of payments, so community pressure is a major incentive to conserve lions. However, critics question the long-term financial sustainability of privately funded compensation and highlight moral hazards such as reduced livestock guarding efforts or payments claimed for other livestock losses (Nyhus et al. 2003; Bulte & Rondeau 2005). Additionally, compensation programs usually have high administrative costs, particularly in communities with poor governance (Nyhus et al. 2003; Maclennan et al. 2009), and people may threaten to kill predators if compensation payments stop (Treves et al. 2009), potentially limiting the long-term sustainability of any conservation success. These programs may remain politically popular because they can improve public support for conservation initiatives (Naughton-Treves et al. 2003), but they are often externally conceived and may overlook values of communities where they operate.

The Lion Guardians (LG) program employs traditional conflict mitigation techniques to reduce livestock depredation and attempts to incorporate community cultural values and belief systems to improve local tolerance of large carnivores (Infield 2001; Stringer et al. 2006). In addition, LG directly monitors lion numbers and movements to further engage communities in wildlife conservation and reinforce the link between the program and large carnivore presence (Dolrenry 2013). The program provides incentives through conservation-related employment, training in literacy and scientific monitoring, and community assistance, all directly linked to the presence of lions. Nonetheless, simply empowering local people is no guarantee of conservation success if programs are hampered by limited community capacity (Nelson & Agrawal 2008) or unequal or limited benefit distribution (Blaikie 2006). Additionally, this model does not directly address the economic costs of livestock losses incurred.

While these 2 approaches differ in important respects, both assume that incentive-based conservation programs can reduce lion killing. We explicitly investigated the extent to which these approaches decrease lion killing, both individually and together. Because potential confounding factors are unavoidable in nonexperimental studies, we used both theory and empirical data to examine lion

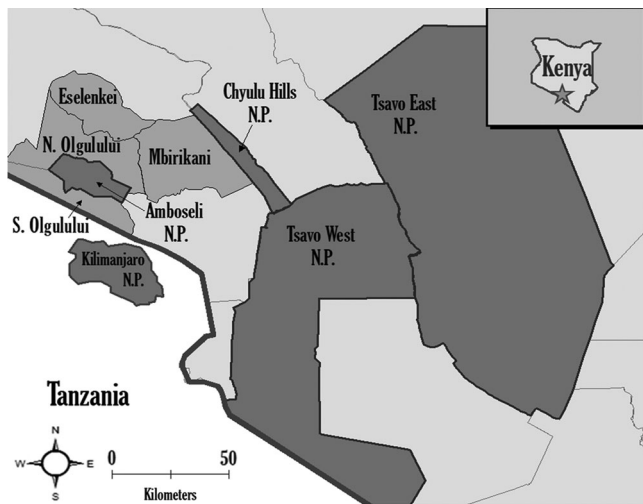


Figure 1. Study areas within the Amboseli-Tsavo ecosystem of southern Kenya.

killing before, during, and after conservation interventions. We identified plausible ranges of causal effects and assessed the implications for carnivore conservation.

Methods

Study Area

The Amboseli Ecosystem is the 5975 km² region between Amboseli, Tsavo West, Chyulu Hills, and Kilimanjaro National Parks (Fig. 1). This region is divided into group ranches, land communally owned by Maasai pastoralists whose livelihood is largely dependent upon livestock (Grandin 1991). Our study area included the group ranches adjacent to Amboseli National Park: Northern (N. Olgulului; 1002 km²) and Southern Olgulului (S. Olgulului; 468 km²), Mbirikani (1229 km²), and Eselenkei (748 km²). Approximately 27,000 Maasai residents and roughly 100,000 heads of livestock live in the 3,500 km² study area (Kenya National Bureau of Statistics [KNBS] 2009).

Conservation Interventions

Both PCF and LG aim to increase tolerance of carnivores and change behavioral outcomes, but they have different origins and methodologies. The PCF program was developed in response to the high rates of lion killing around 2000 and is based on the premise that local people should be compensated for losses incurred by wildlife and that this will reduce motivations to kill lions. The program pays local people market price for depredated livestock (or below if there is evidence of negligence) and imposes penalties for lion killing (MacLennan et al. 2009). Compensation is paid if the livestock carcass is within 1.5 km of the group ranch boundary, reported within 24 h, and

all evidence is preserved (carcass, spoor, drag marks) and verified by PCF officials (MacLennan et al. 2009). To engage the community in decision making, there is an advisory committee of respected Maasai elders. The PCF program relies on rapid verification, economic incentives, and community pressure to produce collective restraint on killing lions. All operational costs and 70% of the livestock payments are paid through private funds, while the group ranch covers 30% of the livestock payments. The program began on Mbirikani in April 2003 and expanded onto neighboring Olgulului (North and South) in August 2008. Eselenkei has no formal compensation program like PCF for livestock depredation.

Emerging from research on Maasai attitudes and motivations for lion killing (Hazzah et al. 2009), Lion Guardians are traditional Maasai *ilmurran*, earning approximately \$100/month. LGs live and work in their home communities and wear traditional clothing, and they fulfill a role akin to the traditional warrior-community protector. The LG program has several incentives for behavioral change, making it difficult to tease apart the main ingredient driving the program. Thus, we present LG as a package of participatory and mitigation tools.

The LG program has 3 main components. First, because the program employs well-respected *ilmurran*, many of whom gained respect by killing lions, it can utilize their traditional leadership roles to prevent lion killing. Upon hearing of a planned lion hunt, guardians attempt to dissuade their peers by stressing the tourism value of lions, the potential threat of arrest, and in some areas the risk of losing PCF payments. They also explain that their own employment is contingent on lion presence in the area, so killing a lion threatens their own livelihood. In Maasai culture, causing problems for another (particularly a respected) community member is frowned upon. Second, because most lion killing occurs in response to livestock depredation, guardians help reinforce *bomas* (livestock corrals), retrieve livestock lost in the bush to prevent further depredation, and inform communities about local carnivore movements. Lastly, guardians provide a sense of community ownership of lions by monitoring lions on community land through traditional methods and radio tracking (Dolrenry 2013).

Lion Mortality Data

All recorded incidents of lion killing occurred between 2003 and 2011, and data were collected between 2007 and 2011. The PCF program began on Mbirikani in 2003; preintervention data from 2001 to 2002 for Mbirikani were only available from the Amboseli-Tsavo Game Scout Association. These data were based on lion carcass counts, thus inferring causality for before and after Mbirikani compensation effects must be done with caution (Heckman et al. 1997).

For all lion mortality data we relied on informants, recruited across the study area, who had no conservation-related employment. They queried their community members about past lion killing events. Direct questioning applied with a snow-ball method (Bernard 1998) was used to identify past lion killers. With help from informants, we compiled a list of individuals with lion names in every community. Each man who had killed a lion since 2003 was asked to recall the details of each hunt and show the location of the kill site.

Each alleged hunt was recounted independently by at least 3 participants who were present at the hunt, and these accounts were compared. Comparable, confirmatory data from multiple sources at different times enabled triangulation to maximize reliability and validity of the data (Bernard 1998). To ensure response accuracy we compared different aspects of each event (e.g., time of day, number of participants, sex of lion, details of kill site) between participants. In addition, we collected any bones from the kill site, identifying them as lion bones by comparing them with skeletal material at the National Museums of Kenya.

People often had difficulty recalling the exact month or year a lion was killed, so the approximate date was reconstructed with reference to a local calendar of events (Freudenberger 1994). Killings by group ranch members outside the study area in neighboring parks or across the border in Tanzania were assigned to the killer's home area because the intention was to test effectiveness of conservation treatments at those original locations. We excluded any mortality where cause of death was natural, unknown, or due to government-sanctioned problem-animal control.

Data Analyses

Empirical inference on intervention effects is a core objective of much conservation evaluation research (Ferraro & Pattanayak 2010). Credible inference is often difficult because measurement errors in data on illicit behavior may be both extensive and systematic (Piquero & Weisburd 2010). We compared the number of lions killed before and after intervention. However, it was impossible to conclusively demonstrate efficacy because the alternative outcomes that would have occurred in the absence of intervention were unknown. Such unobserved effects are known as counterfactuals, and because they cannot be logically observed, the effect size of interest is only partially identified. To make inferences from the data, assumptions need to be made concerning the likely values of counterfactuals, with stronger assumptions yielding more powerful but less credible conclusions. This is known as the law of decreasing credibility (Manski 2007). We adopted 2 complementary approaches to this problem based on a nonparametric, empirical strategy, and a parametric model of the data.

Empirical Strategy

To investigate the total effect of intervention (i.e., PCF and LG combined), we used Manski's (2007) partial identification approach, which places bounds on the likely range of effects rather than attempting to produce a point estimate. This procedure accounts for the fact that we cannot logically observe what would have happened in the absence of intervention and is described more fully in the supplementary material. Briefly, we began by using the observed lion killing data and the weakest possible set of assumptions to produce no assumption bounds on the effect size for each area. These assumed that the number of lions that would have been killed without intervention was between zero and the maximum observed killings per year. Two additional, stronger, assumptions were then applied: a monotone treatment response (MTR), meaning the probability of lion killing in a nonintervention area would not be increased by intervention and a monotone treatment selection (MTS), meaning all areas implemented either or both programs under the assumption that it would reduce lion killing. Combining MTR and MTS tightened both the lower and upper bounds of the assumptions.

Model-Based Strategy

We assessed whether intervention had a significant effect on the number of lions killed using a jackknifed generalized linear model (GLM). The GLM approach strengthens assumptions compared to our empirical strategy because it assumes that the counterfactual distribution matches the distribution inferred from observed values (Manski 2007). Our model evaluated the explanatory power of lion density, year, intervention, area, and rainfall (with density, year, and rainfall as continuous variables). The size of each area was implicit in the area effect. Cultural effects were not considered because all study areas contained only Ilkisonko Maasai pastoralists, with relatively homogenous cultural and traditional beliefs and practices. Sequential model fits, with pairwise comparisons of the likelihood ratio statistic (assumed to follow a χ^2 distribution), were used to test for significance in the covariates.

The model took the form

$$\eta = l\eta(\mu) = \beta_0 + \sum_i x_i \beta_i,$$

where μ is the expected number of lions killed and η follows a negative binomial distribution with dispersion parameter θ (Venables & Ripley 2000). The negative binomial distribution was chosen to represent the count data because it better accounted for overdispersion than a Poisson distribution. The coefficient β_0 is an intercept term, β_i is the predicted effect of covariate i , and x_i is the observed value.

Table 1. Implementation timeline for predator compensation fund (PCF) and Lion Guardians (LG) at each study site.

| Area | Preintervention | PCF start date | LG start and combined with PCF | LG start date |
|--------------|-----------------------|-------------------------------------|--------------------------------|-----------------|
| Mbirikani | 2001–2003 (2.3 years) | April 2003 (3.8 years) ^a | Jan. 2007 (4 years) | |
| N. Olgulului | 2003–2008 (4.7 years) | Aug. 2008 (1.2 years) | Oct. 2009 (2.2 years) | |
| S. Olgulului | 2003–2008 (4.7 years) | Aug. 2008 (2.1 years) | Sept. 2010 (1.3 years) | |
| Eselenkei | 2003–2009 (5.6 years) | N/A | N/A | July 2009 (2.6) |

^aThe PCF was suspended on Mbirikani due to infractions of the agreement from 28 June 2003 to 21 January 2004; from 7 April to 22 June 2005; and from 4 to 12 October 2005 (MacLennan et al. 2009).

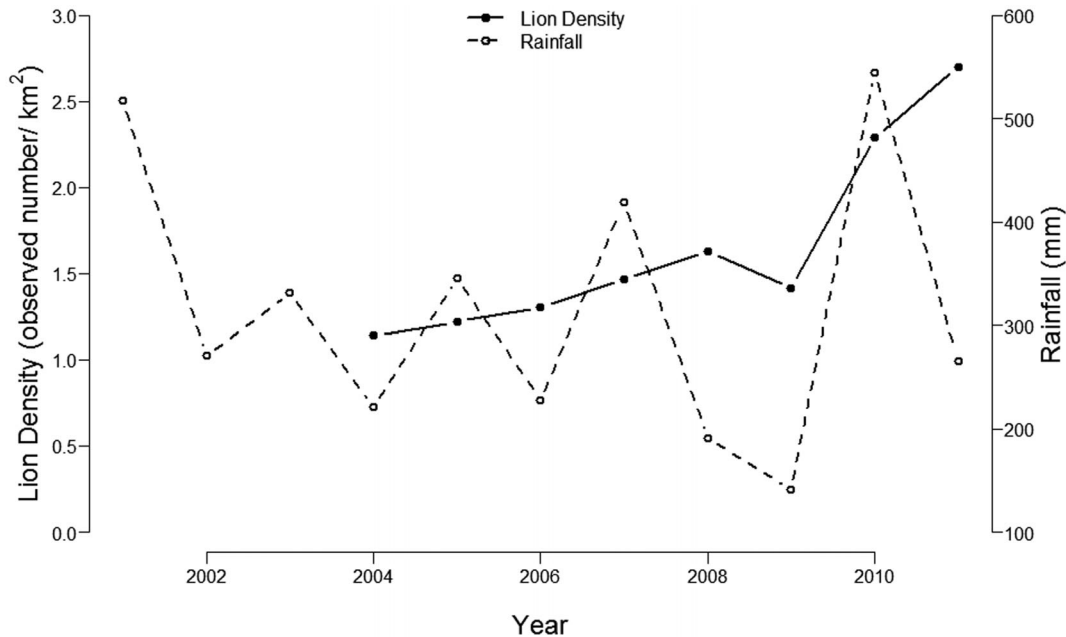


Figure 2. Estimated lion density across the study areas over time and relative to rainfall in 2000–2011 (J. Altmann & S. Alberts, unpublished data).

When fitting to the complete data set, we identified influential observations (S. Olgulului 2010) and therefore used a robust method to estimate the effect size and the significance of intervention. This involved a jackknife procedure in which distributions of unbiased coefficients were obtained from the sequential deletion of each data point in turn, with repeated fits of the GLM (Abdi & Williams 2010). The medians of these distributions provided robust estimates of treatment effect size, which we measured as proportionate reductions in the number of lions killed compared with the no-intervention scenario. Uncertainty in estimates of the median was measured as a standard error using methods described in Bloch and Gastwirth (1968).

The significance of pairwise differences in intervention effects (measured as a p value) were derived through simulation by randomizing the number of lions killed between the 2 interventions and repeating the jackknife procedure. This generated a distribution of median values assuming no effect. The p value was then the null-probability of obtaining an effect size greater than that observed.

Four types of intervention were represented in the data; no intervention, PCF only, PCF and LG combined; and LG only (Table 1). The LG only treatment group was very small (Eselenkei, 2009–11), so we combined this group with the PCF and LG group prior to analysis (Supporting Information). This improvement in parsimony also led to a better model fit.

Results

Lion Density and Rainfall

Lion numbers and behaviors were recorded from 2004 onwards. Regional lion ranges were large (average MCP for males 2848 km², females 954 km²; Dolrenry 2013). We examined lion densities at the ecosystem level since the majority (94.6%; $n = 95$) of adult and subadults monitored during the study period used multiple areas. Lion densities were relatively stable throughout the study period (Fig. 2), with the exception of the 2009 drought, during which lions ranged more widely and more cubs were born in 2010 and 2011 (Dolrenry 2013).

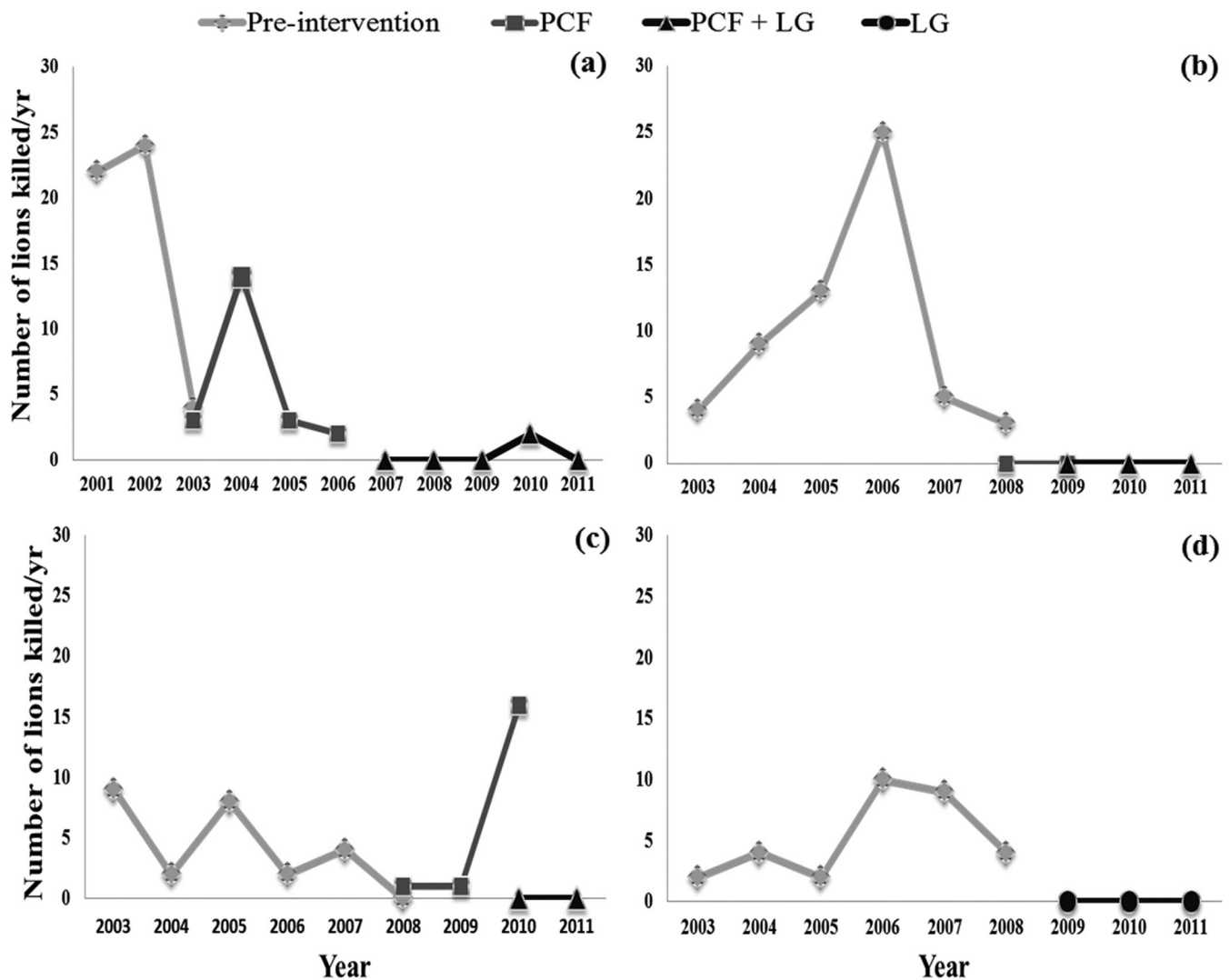


Figure 3. Number of lions killed per year in the Amboseli ecosystem in (a) Mbirikani, (b) N. Olgulului, (c) S. Olgulului, and (d) Eselenkei prior to any intervention, illustrated by different stages of intervention (prior to any intervention, Predator Compensation Fund alone, Predator Compensation Fund and Lion Guardians in combination, and Lion Guardians alone).

Rainfall is highly variable in Amboseli, and the drought of 2008 and 2009 (mean annual rainfall of <190 mm) affected the entire study area, reducing livestock numbers by 65% in 2009 (ACC 2009).

Lion Mortality Data and Trends

Before the study interventions (2001–2002), 46 lions were killed on Mbirikani alone. During the study period (2003–2011) at least 161 lions were killed by Maasai living in the study area. We excluded an additional 29 lion deaths because cause of death was unknown (50%), the lions were legally killed by government (26%), the killer or killers were not members of the study communities (23%), or the deaths were natural (1%). A further 15 alleged kills were excluded due to inconsistencies in reports or an absence of lion bones at the kill site. Fifty-five

percent of killings were reported to be in retaliation for lost livestock, and the remainder were rite of passage and political protest killings. Seventy-eight percent of lions were speared and the remainder poisoned. Retaliation for depredation and protest killings involved both spearing and poisoning, whereas all lion killing by warriors to gain prestige involved only spearing. The lowest levels of lion killing (mean of 2 lions killed per year) and highest rates of livestock depredation by carnivores recorded coincided with the drought period (2009; PCF, unpublished data).

Observed Area Relationships and Patterns

Both PCF and LG were first implemented on Mbirikani (April 2003 and January 2007, respectively). Prior to the start of PCF (2001–2003), the rate of lion killing averaged 21.7 per year (Fig. 3a). Compensation alone was

Table 2. Results of empirical bounding analysis of the number of lions killed under the combined effect of predator compensation fund and Lion Guardian interventions.*

| | | No | MTR | MTS | MTR + MTS |
|--------------|-------|------------|--------|--------|--------------|
| | Bound | assumption | | | |
| Mbirikani | lower | -21.37 | -21.37 | -19.01 | -19.01 |
| | upper | 2.63 | 0.00 | 2.63 | 0.00 |
| N. Olgulului | lower | -16.00 | -16.00 | -10.54 | -10.54 |
| | upper | 9.00 | 0.00 | 9.00 | 0.00 |
| S. Olgulului | lower | -6.82 | -6.82 | 0.83 | 0.83 |
| | upper | 9.18 | 0.00 | 9.18 | 0.00 |
| Eselenkei | lower | -6.22 | -6.22 | -4.77 | -4.77 |
| | upper | 3.78 | 0.00 | 3.78 | 0.00 |

*Given a partially identified problem it was not possible to estimate the effect size unless we made assumptions about the likely influence of the effect. In this empirical analysis, we made a very weak set of assumptions that can yield only a range of possible values. The no assumption bounds represented the weakest possible assumptions that could be made, specifically that the counterfactual (unobservable) expectation was between zero and the maximum value observed for that area. The MTR and MTS represented increasingly stringent assumptions that allowed us to make stronger conclusions regarding the range of likely effect sizes. Further details on this approach are given in the Supporting Information.

associated with a 73% reduction in lion killing on Mbirikani (average 5.8 lion deaths per year after implementation, 3.8 years). The combination of hiring of 8 guardians in 2007 and PCF was associated with a further decline of 91% (less than one killed per year) in lion killing compared with years with compensation alone.

The PCF program expanded to both Olgulului regions at the onset of the drought in August 2008 in response to high levels of lion mortality, averaging 12.5 lions killed per year from 2003 to 2008, with 25 lions killed in 2006 alone. No lions were killed on N. Olgulului during the 1 year PCF operated alone. In October 2009 the LG program was implemented on N. Olgulului, 8 guardians were employed. Reduced lion mortality was sustained; no lions were killed from 2009 to 2011 (Fig. 3b). On N. Olgulului, lion depredation on livestock increased 5-fold after the drought broke in early 2010, making the lack of lion killing even more striking, particularly relative to S. Olgulului.

In S. Olgulului, PCF operated independently of LG for 2 years. Prior to PCF, the average numbers of lions killed was 4.2 annually. Once PCF was initiated the average number of lions killed increased to 6 lions annually. This slight increase was primarily due to 16 lions killed in 6 months in 2010 by S. Olgulului members (Fig. 3c). LGs were introduced in September 2010 alongside PCF, and no additional lions were killed during the study period.

Between January 2003 and June 2009, 31 lions were killed by Eselenkei residents (5.6 per year). In July 2009 LG was initiated on Eselenkei, the only group ranch in the study area without formal compensation. Although the sample size was small, it was linked to a substantial

Table 3. Estimates of the effect size of conservation interventions measured as proportionate reductions in the number of lions killed compared with that expected under no intervention from a generalized linear model fit to the data.*

| Intervention | Naive estimate | Robust estimate | SE | p |
|--------------|----------------|-----------------|------|---------|
| PCF | 0.87 | 0.91 | 0.26 | 0.0390 |
| LG + | 0.99 | 0.99 | 1.18 | <0.0001 |
| LG/PCF | | | | |

*Effect size is a proportionate reduction in the number of lions killed compared with that expected if there were no intervention. The naive estimate corresponds to the model output with all the data included. The robust estimate is a median value from repeated application of the model to jackknifed data sets. The difference between the 2 is an indication of the bias inherent to the data set, which is corrected by the robust approach. Standard errors and p values are for the robust estimate.

decline in killings. No lions were killed on Eselenkei after LG inception (Fig. 3d).

Empirical Strategy

The bounding analyses (Table 2) indicated that conservation interventions on Mbirikani reduced, on average, the number of lions killed by 0–19 (the upper and lower bounds of the combined assumptions). For N. Olgulului, conservation interventions resulted in avoided lion mortality of 0–10.5 lions. In Eselenkei conservation intervention avoided from 0 to 5 lion deaths. Even though these are the worst case bounds and the range was large for some areas, all identified ranges were negative for the average number of lions killed, indicating that conservation interventions reduced lion killings. Conversely, the S. Olgulului range interval was positive, with an average of 0–1 lions killed; conservation intervention was ineffective in this area, likely due to the spike in killing in 2010.

Model-Based Approach

Sequential model fits (Supporting Information) demonstrated that the most parsimonious model included lion density, intervention, and area as explanatory variables (Table 3). Lion density had greater explanatory power than year, and rainfall was not significant. Significant interaction terms could not be discerned.

The model estimated that PCF resulted in an 87–91% decline in the number of lions killed. The model outputs also estimated that LG, operating in combination with PCF and alone, resulted in a 99% decline in the number of lions killed.

Discussion

Whether compensation and participatory programs improve attitudes toward wildlife has been investigated (Naughton-Treves et al. 2003; Mutimukuru et al. 2006;

Agarwala et al. 2010), but the long-term effectiveness of both programs running in the same area have seldom been evaluated with empirical data. This study presented a unique opportunity to observe these 2 approaches as strategies for managing a complex conservation problem. Both programs were robust, carefully designed, and implemented with rigor within their respective but divergent contexts, but they used different incentives: PCF is based primarily on an economic model of behavior, while LG draws more on traditional Maasai values. Our results indicated that both approaches contributed to a measurable and statistically significant decrease in lion killing.

Relationship between PCF and Lion Killing

When used alone, compensation was associated with a marked reduction in lion killing, implying that at least some Maasai pastoralists value monetary compensation for livestock losses enough to change their behavior. However, there were still episodes of lion killing, the first when PCF was first implemented on Mbirikani (22 lions killed in 3.5 years) and the second when 16 lions were killed in S. Olgulului in the first half of 2010. S. Olgulului did not experience disproportionate levels of livestock depredation compared with other study areas during this time (PCF, unpublished data). Furthermore, Maasai living in other areas exhibited comparable hostility toward lions in response to the postdrought increase in predation: 45 retaliatory hunts were attempted in the other study areas in 2010 but were stopped by LGs and rangers. In the absence of LG, S. Olgulului hunts continued despite the presence of rangers.

The 2010 S. Olgulului hunts may have been motivated in part by the withholding of compensation payments due to an unpaid fine on the local community for killing a lion. In areas where communities have long-standing resentment toward conservation, withholding payments due to infractions maybe be politically fraught, all the more so if an entire community is penalized for the illicit actions of a few individuals (Jackson & Naughton-Treves 2012). Maasai in Kenya have long used wildlife killing as a political strategy (Western 1982; Lindsay 1987), and 2 lionesses were killed on Mbirikani in early 2010 to enforce demands for higher compensation payments.

Despite the 2 spikes in killings, compensation was associated with reduced lion killing over time. The PCF program is better designed than many other compensation schemes (Treves et al. 2009; Agarwala et al. 2010; Boitani et al. 2010) and offers timely verification and payments, sanctioned penalties for poor husbandry, and local involvement through an advisory committee (MacLennan et al. 2009). Although PCF on its own clearly improved conservation outcomes, during this study the PCF-LG combination and LG operating alone were most effective.

Relationship between LG and Lion Killing

LGs were associated with near-total cessation of lion killings in each area where it was implemented. Even at a time of high livestock depredation, no lions were killed after the drought broke in 2010 on Eselenkei, where LG operated without PCF. On S. Olgulului, no further lions were killed after the LG program was initiated in 2010. This finding may be explained by the program's emphasis on the role of the *ilmurran* in Maasai culture and efforts to connect cultural values to conservation goals (Infield 2001). Tying lion conservation goals to the provision of modest but regular wages for influential (and lion killing) men in the community may also be a key factor in reducing lion killing.

A further possible explanation is that LGs also protect cattle. For example, in 2012, guardians recovered 11,240 lost livestock worth over \$1,000,000 and reinforced 350 livestock bomas (50% were resampled and 90% of these stated no further depredation). While completing their duties, guardians also found 18 lost child herders. LG consistently respond to nascent conflict situations (e.g., when guardians find fresh carnivore signs or nearby radio-telemetry signals they warn herders to avoid these potentially high-risk areas). After a boma has suffered depredation, they work with the livestock owner to reinforce and strengthen the enclosure. Collaboration between local scouts and livestock owners in conflict sites elsewhere has improved participation and reduced moral hazards (Jackson & Wangchuk 2001). There are, however, limits to emphasizing cultural traditions and participatory schemes to save large carnivores. In many areas indigenous communities do not value large carnivores in a way that can be translated to a warrior protectionist model. Also, the benefits and outcomes of participatory conservation programs (e.g., ownership of resource, increased tolerance) may be slow to reach the broader community. However, once they are established and entrenched in the local value system, these benefits may be long lasting (Brown 2003).

Potential Costs and Benefits of the Interventions

Both PCF and LG reduced lion killing; however, the LG-PCF combination plus LG alone was associated with a greater decline. LGs are all employed from within the community and continue to live and work with community members. Critically, compensation does not diminish the frequency of depredation but is a response mechanism to depredation, with effort applied to preventing hunts through peer pressure with the threat of loss of payments. The LG program specifically aims to reduce depredation incidents and, when hunts are planned, attempt to intervene. This preemptive strategy may itself lower conflict levels and motivations to kill lions. However,

LG does not offer a postdepredation response except to reinforce the affected boma.

Moreover, the LG model appears more cost effective: PCF costs approximately \$250,000/year (approximately 1700 claims per year) and employs 30 community members in a 2699 km² area (\$92.63/km²/year), while LG costs approximately \$140,000/year and employs 38 community members in a 3447 km² area (\$40.62/km²/year). Furthermore, lasting economic sustainability is a common concern regarding compensation, with fears of retributive killing from community members if payments cease (Wagner et al. 1997; Nyhus et al. 2003). Such concerns could also be raised with the LG model in regards to previous lion killers turned LGs; these people may return to killing if they ceased being employed. Yet, 15 guardians have been dismissed and none are known to have returned to lion killing. Our conclusions are based on a relatively short period, and although our results are compelling, circumstances change, particularly in an area of increasing human population and changing cultural norms. Thus, it is imperative for any community conservation program to consider long-term financial sustainability and careful exit strategies before implementation.

In designing conservation interventions to reduce killing of problem wildlife species by local people, we recommend consideration of participatory programs that encompass traditional noncash cultural values and ones with a more direct economic intervention. Where compensation programs currently exist, additional participatory prevention components that share the same conservation objectives may prove effective (Boitani et al. 2010). In this way a greater range of incentives, benefits, and community values may be utilized to achieve conservation goals.

Other incentive-based schemes beyond these 2 approaches deserve consideration. Direct performance payments to livestock owners (e.g., paying for live lions), may avoid many of the perverse incentives of compensation that lead to poor livestock care and moral hazard (Ferraro & Kiss 2002; Nelson 2009). While the search for effective, sustainable strategies for human-carnivore coexistence continues, there is a growing consensus that part of the solution requires greater involvement of local people. Conservationists cannot always rely upon a single conservation incentive; rather, they should consider a broader and more flexible approach that is tailored to the specific values and culture of the relevant local communities.

Acknowledgments

We thank all the participating group ranch communities for their collaboration on this study. This research was conducted with the permission of the Government of Kenya (MOEST 13/C689) and Kenya Wildlife Service. It was funded by Panthera,

Fulbright-Hays DDF, and the University of Wisconsin-Madison (Lawry Fellowship). Additional support was provided by the Flora Family Foundation, the Rufford Foundation, S. Gold, the Philadelphia, San Francisco, and Denver Zoos. We thank S. MacLennan, MPT staff, and ATGSA for information on lion killing and lion depredation. We also thank A. Jain, C. Manski, L. McDonald, and D. Kaplan for their statistical advice. The rainfall data were collected by the Amboseli Baboon Research Project with support from NSF (BCS-0323553, IOS-0919200); we thank S. Alberts and J. Altmann for permission to use them. We especially thank L. Mammai for his critical field assistance and P. Briggs and the LG. This manuscript was substantially improved by comments from A. Dickman, G. Balme, V. Fishlock, F. Nelson, and P. Ferraro.

Supporting Information

GLM sequential model fits (Appendix S1), model coefficients (Appendix S2), boxplot of lion killing in all areas distributed by year and intervention status (Appendix S3), and the bounding analysis description (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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