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**The Effect of Predator Culling on
Livestock Losses:
Ceres, South Africa, 1979 – 1987**

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Abstract

Caracals (*Caracal caracal*) and leopards (*Panthera pardus*) are perennial problems for sheep farmers on the southern fringe of the arid Karoo. In the past, farmers responded to the conflict with blanket culling of predators, a strategy which ecologists understand to be harmful. This paper investigated the ability of blanket predator culling to reduce livestock losses. It found the probability of livestock losses to be a function of the number of caracals, leopards, vagrant dogs (*Canis familiaris*) and other wildlife culled during the previous year, as well as the previous year's trapper effort, the farm's remoteness and three years' worth of rainfall. Other unobserved farm characteristics did not systematically affect losses. Culling an additional caracal or leopard was estimated to increase future livestock losses by 5.7% and 27.2% respectively, while culling a vagrant dog was estimated to reduce the likelihood of future losses by 9.5%. Both trapper effort and remoteness increased the probability of livestock losses. The current and previous years' rainfall decreased the likelihood of future losses, while rainfall from two years prior was positively correlated with future losses. These results are important because they describe general culling effectiveness under a variety of management conditions over a period long enough to allow for adjustment to culling.

Introduction

Human-wildlife conflict is as much a conflict between humans with differing convictions, as it is a conflict between humans and animals (Treves and Karanth, 2003). In sheep farming, the conflict occurs between ecologists who consider culling unnecessary and harmful and farmers who insist on culling as the main strategy for protecting their livelihoods.

Culling is thought to be harmful to the environment and to farming interests because it actually increases predator densities while attempting to decrease them. Heavily culled coyote (*Canis latrans*) populations differ from natural populations insofar as they are characterised by younger first breeding ages, larger proportions of breeding betas, larger litter sizes, better pup survival and higher rates of in-migration (Knowlton, 1972; Andelt, 1985; Gese et al., 1989; Crabtree, 1997; Crabtree and Sheldon, 1999; Knowlton et al., 1999). Similar demographic compensation has been reported for black-back jackal (*Canis mesomelas*) (Bingham and Purchase, 2002), caracals (*Caracal caracal*) (Marker and Dickman, 2005) and gray wolves (*Canis lupus*), amongst others (Sidorovich et al., 2007). It can therefore be said that the more farmers cull, the bigger their predation problem is likely to become. In addition, culling is considered ecologically unnecessary because it replaces natural mortality processes (Knowlton, 1972; Gese et al., 1989) and often indiscriminately kills the wrong individuals (Sacks et al., 1999). A study of coyote-sheep interactions revealed 92% of sheep kills in one year, and 80% of sheep kills in another, to have originated from a single coyote breeding pair (Sacks et al., 1999). Till and Knowlton (1983) linked sheep killing to the provisioning of pups and showed that killing could be stopped by removing the pups from the den or culling the breeding pair only.

This paper investigated the impact of culling on farming interests *per se*, rather than its impact on the environment. Given the significance of predation as source of risk to the small stock industry (Knowlton et al., 1999; Mitchell et al., 2004), it is vital that farmers understand the harm they may be doing to their own financial interests through blanket culling; of course getting farmers to change their behaviour would also bring about potentially important environmental benefits.

Recent studies of human-wildlife conflicts have either investigated farmers' tolerance of wildlife (e.g. Holmern et al., 2007; Stronen et al., 2007; Thorn et al., 2012) or explained farm-level livestock losses (e.g. Dar et al., 2009; Thorn et al., 2012). Thorn et al. (2012) was one of the few papers to combine these two ideas, but it modelled the probability of using lethal control rather than the level of livestock losses. Here we drew on Conner et al. (1998) to model the

probability of livestock losses as a function of historical culling at the species level, while explicitly controlling for several other factors known to affect livestock losses.

Methodology

Study Area and Available Data

The domain of the ‘Ceres South Hunting Club’ was selected as the study area due to the quality of the culling records kept by the club. We extracted from the club’s logbooks a panel dataset covering 152 farms for the period 1979 to 1987.

Ceres lies on the northern side of the Cape Fold Mountains on a transition from Fynbos to Succulent and Nama Karoo Biomes (Muchina and Rutherford, 2006). Aggregate data represent Ceres as a primarily fruit farming district (Statistics South Africa, 1981; Conradie et al., 2009), but the Karoo portion of the district is only suitable for sheep farming. Wool sheep were the dominant type of livestock kept in Ceres during the study period, accounting for more than 90% of the district’s livestock holdings in 1981 (Statistics South Africa, 1981). The average size of sheep farms in Ceres was not recorded in the farm census but can be inferred from neighbouring Laingsburg to have been in the order of 4 800 hectares and 825 breeding ewes per farm in 1981 (Statistics South Africa, 1981).

In the 1980s, hunting clubs were government-supported and regulated. The Ceres club employed a fulltime trapper plus two assistants. This team responded to stock loss events, usually sheep or lambs caught by caracals or leopards. Their culling methods included gin trapping, baited cage trapping, hunting with and without dog packs, and the use of coyote getters. Usually visits continued until the problem animal(s) were found. In addition, the trapper routinely monitored problem farms on which he did some preventative trapping. Meticulous handwritten records were kept of each visit, including farm identifier, name of contact person, date, distance travelled, number and type of stock losses (sheep, lambs, goats), number of predators culled (caracal, leopard, black-backed jackal, feral dog (*Canis familiaris*)), number of innocent animals killed (e.g. porcupine, hares, small antelope, African wild cat, silver fox) and culling method used. The logbooks contained brief case descriptions of unusual events from which it was inferred that the official trapper was responsible for most of the predator management on most farms. Lacking evidence to the contrary, we assumed that he worked on all farms in his area at least once during the study period.

Data Transformations

Daily logbook entries were digitised to compile annual stock loss and culling statistics for each farm. A rainfall variable (E2B) was appended to the dataset from Midgley et al. (1994). We assumed a unique combination of farms' and owners' names to indicate unique farms. The majority of entries were null, meaning that the trapper had no dealings with these farms in these years. Most of the remaining farms reported easily classified single incidents. A small proportion of records consisted of multiple incidents involving different predators during the course of a year. For such farms the full list of incidents was inspected to establish the dominant type of predator problem; where it was impossible to do so, predator type was indicated as multiple.

The dataset was restricted to pure livestock-wild predator interactions by constructing three dummy variables, one each for baboon (*Papio ursinus*), stock theft and vagrant dog incidents. Vagrant dogs killed significantly more livestock (14.72 sheep) per incident than was lost per incident (1.05 sheep) to all other problems ($t_{1366}=-13.45$, $p=0.000$). Similarly, stock theft caused larger (34.00 sheep) losses than all non-theft incidents (1.33 sheep) ($t_{1366}=-12.03$, $p=0.000$). For baboon incidents, there was no difference in the number of sheep lost ($t_{1366}=0.86$, $p=0.3894$), but they triggered more visits (8.93) than non-baboon incidents (1.68 visits) ($t_{1366}=-5.12$, $p=0.000$). Baboon problems accounted for 2% of all trapper visits, and stock theft and vagrant dog incidents for 0.4% and 3% of visits respectively. The restricted sample size was 1 293 observations.

Finally, we constructed a variable for 'all other' animals culled, which included baboons and porcupines culled in response to crop damage, accidental culling (e.g. of small antelope, hares, etc.) and inappropriate culling of innocent animals (e.g. Cape fox (*Vulpes chama*) and African wildcat (*Felis libyca*)).

Modelling

We specified three stock loss models, namely a pure culling response model of Conner et al. (1989), a prey-predator dynamics model based on the ideas of Sacks and Neale (2007) and a third model which combined the culling response and trophic dynamics sub-models. Using annualised data, Conner et al. (1998) established trapper effort to be positively correlated with reported livestock losses, and the number of coyotes culled to be positively correlated with trapper effort, but they failed to find a significant relationship between coyotes killed and the following year's stock losses. If culling was effective, more predators culled in year t should lead to fewer stock losses in year $t+1$, while a positive and significant relationship between the two would indicate predator population

compensation. Running the Conner et al. (1989) model on the first two years of this dataset, Conradie (2012) failed to result in a statistically significant coefficient on the feedback effect.

Both Conner et al. (1989) and Sacks and Neale (2007) described situations where a single predator (coyotes) preyed on sheep. At least three predators were important in Ceres in the 1980s. Many other animals were killed accidentally or because they were believed to kill lambs, when in fact they were not doing so. We found that specifying culling at the species-level for caracals, leopards and dogs was able to explain the variation in livestock losses better than aggregate culling. Including all other culling as a fourth variable further increased the explanatory power of the model. Specifying the number of baboons culled separately did not materially affect results. We controlled for trapper effort and defined effort as the number of visits to a given farm in a given year. Both the predators culled and trapper effort variables were lagged by one year (Berger, 2006; Sacks and Neale, 2007) and squared terms were included to allow for nonlinear relationships for the variables of interest.

Culling response sub-model:

$$\begin{aligned}
 \text{Stock losses}_t = & a_0 + a_1 \text{caracal culled}_{t-1} + a_2 (\text{caracal culled})_{t-1}^2 + a_3 \text{leopard culled}_{t-1} \\
 & + a_4 (\text{leopard culled})_{t-1}^2 + a_5 \text{vagrant dogs culled}_{t-1} + a_6 \text{other animals culled}_{t-1} \\
 & + a_7 \text{trapper effort}_{t-1} + a_8 (\text{trapper effort})_{t-1}^2 + a_9 \text{stock losses}_{t-1} + \varepsilon
 \end{aligned}
 \tag{1}$$

We considered catch per effort as an alternative way to estimate predator density (Knowlton, 1972) but decided against using it because we were interested in the effect of human presence in the environment when controlling for number of predators culled. In the Karoo, the folk theory of predator behaviour states that predators are deterred by human presence; therefore the more remote a farm is, the lower its human density and the more suitable it would be as a predator habitat (see Woodroffe, 2000). A time invariant remoteness variable was generated from the distance between the trapper's base in town and individual farms.

The Sacks and Neale (2007) model of trophic dynamics found sheep losses to be negatively related to current season's plant productivity and positively related to current season predator density, while the current season predator density was found to be positively related to the previous season's primary plant productivity. We had very little with which to model trophic dynamics. Space invariant rainfall in year t was used as a proxy for primary plant productivity, while lagged rainfall was tried as a (weak) proxy for predator density. Following Sacks and Neale (2007), the sign on the current rainfall variable was expected to

be negative, because an abundance of natural prey in a good year would keep livestock relatively safe. Sacks and Neale (2007) argued the expected sign on lagged rainfall to be positive, as a good year would cause an increase in predator density which would cause more stock losses the next year. In addition, we included a two-year rainfall lag to be able to investigate the adjustment process beyond just one year.

Trophic dynamics sub-model:

$$\begin{aligned}
 \text{Stock losses}_t = & a_0 + a_1 \text{remoteness} + a_2 (\text{remoteness})^2 + a_3 \text{rainfall}_t + a_4 (\text{rainfall})_t^2 + a_5 \text{rainfall}_{t-1} \\
 & + a_6 (\text{rainfall})_{t-1}^2 + a_7 \text{rainfall}_{t-2} + a_8 (\text{rainfall})_{t-2}^2 + a_9 \text{stock losses}_{t-1} + \varepsilon
 \end{aligned}
 \tag{2}$$

Model 3 simply combined the previous two. The dependent variable in all three models was total stock losses, defined as the number of sheep, lambs, kids or goats lost and ranging from zero to a maximum of 114.

The lagged stock loss variable was added in all three models to check for adequate specification. Ideally it would be insignificant as significance would indicate systematic differences across farms that were not captured by the specification in question.

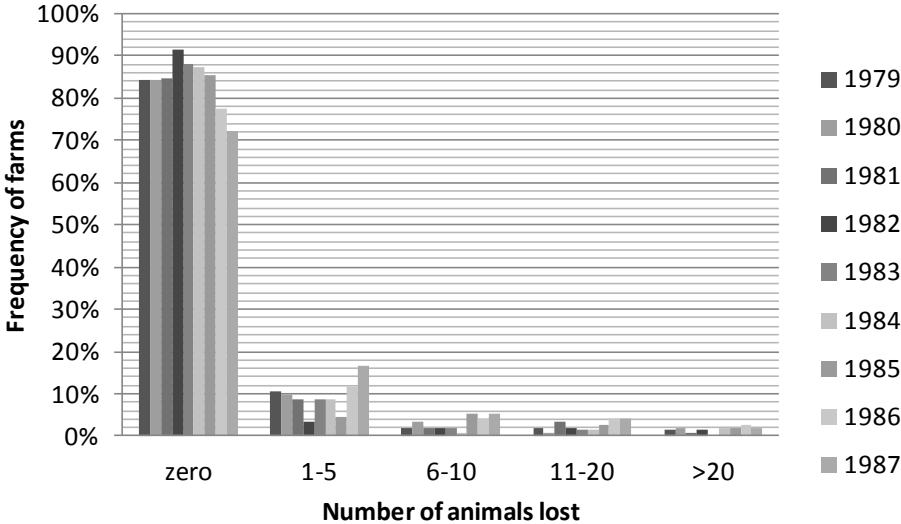


Figure 1: Incidence of livestock losses, Ceres hunting club 1979 to 1987

The frequency of farm-level livestock losses per year, illustrated in Figure 1, clearly called for the use of a limited dependent absence/presence model such as binary logit. The logit model,

$$\log\left(\frac{P_{it}}{1 - P_{it}}\right) = X\beta_i + \varepsilon_{it}$$

where p_{it} = probability of experiencing livestock losses on a given farm in a given year, was estimated in Stata10 from a pooled dataset with a maximum likelihood routine. A Huber-White sandwich estimator was used to account for heteroskedasticity (Baum, 2006). Given the distribution of the dependent variable, we also experimented with Poisson and negative binomial regressions (Gujarati, 2003; Thorn et al., 2012) but rejected these functional forms based on poor maximum likelihood statistics.

Results

Descriptive Statistics

Table 1 summarises the descriptive statistics. The majority of farms experienced zero stock losses and culled no predators in most years of the study period. The mean number of losses per farm was 1.48 livestock units, and the mean incidence rate, expressed as the proportion of farms experiencing losses, was 16%. The incidence rate varied from 9% in 1982 to 28% in 1987. The highest number of losses per farm in a given year fluctuated considerably from a low of 14 sheep recorded in 1983 to a high of 114 sheep recorded in 1985. Total losses during the study period came to 1983 livestock units, with a value of almost R1.2 million (US\$133 000) in 2010 prices. The financial impact demonstrates that this problem should be taken very seriously.

In the study period, 217 caracals and 32 leopards were culled in the area, giving mean culling rates of 0.16 caracals and 0.02 leopards per farm per year. The maximum number of individual animals culled on any farm in any year was three leopards and 11 caracals. Black-backed jackal problems were recorded on only two occasions, when two and three animals respectively were culled. The maximum number of vagrant dogs culled on any farm in any year was four, while the mean rate of culling was 0.03 dogs per farm per year. The maximum and mean numbers of baboons culled were 29 and 0.12 respectively per farm per year. The maximum and mean distances travelled by trappers were 140 and 49 kilometres respectively. The mean trapper effort of 1.83 visits varied from zero to 116 visits per farm per year. The farm which got the most attention received

116 visits (in 1979) in response to a single disastrous jackal attack which killed 24 lambs in one night. The second highest level of effort was observed in 1985 when 80 visits were made to a farm in response to a total of 114 livestock losses during the course of the year. Recorded rainfall varied from 146 millimetres in 1979 to 337 millimetres in 1987, with a mean annual precipitation of 240 millimetres over the study period.

Table 1: Descriptive statistics pooled

Variable	n	Mean	Standard deviation	Minimum	Maximum
Livestock losses	1368	1.478	6.977	0	114
Caracals culled	1368	0.159	0.774	0	11
Leopards culled	1368	0.023	0.194	0	3
Vagrant dogs culled	1368	0.029	0.246	0	4
All predators culled	1368	0.213	0.927	0	14
Baboons culled	1368	0.121	1.263	0	29
Innocents culled	1368	0.119	1.036	0	33
Distance from town (km)	1368	49.93	31.81	1	140
Trapper visits	1368	1.827	7.350	0	116
Rainfall (mm)	1368	240.33	57.53	146	337

Most pair-wise correlations between the explanatory variables were mild or low, as can be seen in Table 2. The correlation of $r=0.614$ between predators culled and trapper effort is an unsurprising exception, as we have already explained that stock losses typically triggered culling (Conner et al., 1998; Conradie, 2012). For the same reason, the correlations between trapper effort and leopards ($r=0.378$) and caracals ($r=0.740$) culled were also strong. Trapper effort was not strongly correlated with the number of vagrant dogs culled ($r=0.175$) or the number of innocent animals culled ($r=0.119$). In multivariate modelling, multicollinearity is sometimes raised as a concern, but no remedy is usually available as coefficients estimated in the presence of multicollinearity are still best and unbiased (Gujarati, 2003). High degrees of collinearity produce coefficient estimates with large variances and covariances, which in practice results in variables being dropped from models because they are not statistically significant.

Table 2: Correlation matrix

	Stock losses_{it}	Leopards culled_{it-1}	Caracals culled_{it-1}	Dogs culled_{it-1}	Other culled_{it-1}	Predators culled_{it-1}	Trapper effort_{it-1}	Distance_i	Rain_t	Rain_{t-1}	Stock_{it-1}
Stock losses _{it}	1.000										
Leopards culled _{it-1}	0.125	1.000									
Caracals culled _{it-1}	0.130	0.307	1.000								
Dogs culled _{it-1}	0.060	0.083	0.110	1.000							
Other culled _{it-1}	0.003	0.032	0.112	-0.006	1.000						
Predators culled _{it-1}	0.204	0.315	0.591	0.103	0.060	1.000					
Trapper effort _{it-1}	0.170	0.378	0.740	0.175	0.119	0.614	1.000				
Distance _i	0.026	0.022	0.073	-0.053	0.015	-0.006	0.012	1.000			
Rain _t	-0.100	-0.001	0.015	-0.009	-0.017	0.003	0.030	0.000	1.000		
Rain _{t-1}	0.038	0.006	0.006	-0.032	-0.022	0.032	-0.016	-0.000	-0.583	1.000	
Stock _{it-1}	0.146	0.373	0.295	0.328	0.004	0.212	0.392	0.013	-0.062	-0.000	1.000

Regression Results

Regression results are presented in Table 3. All three models passed Wald's likelihood ratio joint specification tests. McFadden's pseudo R^2 identified the combined model as the preferred one, a conclusion supported by both Akaike's and Schwarz's Bayesian information criteria. The non-significance of the lagged losses coefficient in models 1 and 3 indicated unobserved farm effects to not systematically affect livestock losses. This is not true of model 2, where the coefficient on lagged losses was positive and significant at $p \leq 0.05$.

The coefficients on caracals and leopards culled were positive and significant at $p < 0.01$ in the culling response sub-model. At the mean, the marginal effect of culling an additional caracal was a 7.4% increase in the probability of suffering stock losses during the next year. This impact decreased at a rate 0.7% per additional caracal culled. As leopard culling was a relatively rare event, the marginal effect of culling a leopard was to increase the likelihood of subsequent losses by 16% at the mean. The lack of significance on the squared term of leopards culled implied its marginal effect to be constant. The vagrant dogs coefficient was negative and significant at $p \leq 0.10$, which suggested vagrant dog culling to have been effective. The coefficient on the 'other animals culled' variable was negative but not significant. Trapper effort and its squared term both produced significant coefficients at $p \leq 0.01$ in model 1. Additional effort increased the likelihood of a farm suffering losses during the next year by 1.1% at the mean, while marginal effect of the squared term indicated this impact to decrease at a rate of 0.009% per additional visit.

In model 2, the coefficients on the remoteness variables, distance and distance squared, were both significant at $p \leq 0.01$. An additional kilometre out of town increased the likelihood of subsequent stock losses by 0.4% and this effect was expected to decrease at a rate of 0.0256% per kilometre. The coefficient on rainfall in year t was negative and significant at $p \leq 0.01$. The marginal effects signalled a 1.2% decrease in the probability of livestock losses for every millimetre above mean rainfall and the effect to dissipate at a rate of 0.0219% per millimetre. The coefficient on rainfall in year $t-1$ was not significant in model 2. In contrast, the coefficient on rainfall in year $t-2$ was positive and significant at $p \leq 0.01$. Marginal effects indicated the probability of losses in year t to increase at a rate of 0.7% per additional millimetre above the mean rainfall and for the marginal effect to decrease at a rate of 0.013% per millimetre.

Table 3: Estimation results for pooled logit models explaining farm-level stock losses

	Culling response		Trophic dynamics		Combined	
	Coef. RSE	Marginal effect	Coef. RSE	Marginal effect	Coef. RSE	Marginal effect
Caracals culled _{it-1}	0.702*** 0.266	0.074			0.599** 0.303	0.057
(Caracals culled) ² _{it-1}	-0.070*** 0.026	-0.007			-0.070* 0.036	-0.007
Leopards culled _{it-1}	1.522* 0.836	0.160			2.886*** 1.097	0.272
(Leopards culled) ² _{it-1}	-0.222 0.385	ns			-0.936 0.602	n.s.
Dogs culled _{it-1}	-0.790* 0.475	-0.083			-1.003* 0.516	-0.095
Other culled _{it-1}	-0.254 0.206	ns			-0.470* 0.258	-0.044
Trapper effort _{it-1}	0.103*** 0.037	0.011			0.094* 0.050	0.009
(Trapper effort) ² _{it-1}	-9.10e-4*** 3.11e-4	-9.57e-5			-1.96e-4 7.15e-4	n.s.
Distance _i			0.043*** 0.012	0.004	0.031** 0.013	0.003
(Distance) ² _i			-2.49e-4*** 9.14e-5	-2.56e-5	-1.71e-4* 9.37e-5	-1.62e-5
Rainfall _t			-0.119*** 0.043	-0.012	-0.140*** 0.005	-0.013
(Rainfall) ² _t			2.12e-4** 8.36e-5	2.19e-5	2.50e-4*** 9.07e-5	2.35e-5
Rainfall _{t-1}			-0.048 0.032	n.s.	-0.066* 0.036	-0.006
(Rainfall) ² _{t-1}			9.31e-5 6.35e-5	n.s.	1.29e-4* 7.06e-5	1.22e-5
Rainfall _{t-2}			0.067*** 0.021	0.007	0.084*** 0.024	0.008
(Rainfall) ² _{t-2}			-1.32e-4*** 4.22e-5	-1.36e-5	-1.62e-4*** 4.67e-5	-1.52e-5
Losses _{it-1}	-4.76e-5 0.011		0.026** 0.012	0.003	-0.003 0.014	ns
Constant	-2.151*** 1.000		10.48* 5.986		13.51** 6.580	
n	1149		1005		1005	
Wald LR test	$\chi^2=56.55$	***	$\chi^2=46.57$	***	$\chi^2=80.77$	***
McFadden's R ²	0.0899		0.0646		0.1370	
Log likelihood	-408.58		-370.91		-342.18	
Akaike's	873.15		761.82		720.36	
Schwarz's Bayesian	887.62		810.95		808.79	

*** significant at $p \leq 0.01$, ** significant at $p \leq 0.05$, *significant at $p \leq 10\%$

In the combined model, patterns of significance and magnitude of marginal effects were similar to those of the two sub-models discussed above. For example, the positive signs on predators culled were confirmed for caracals and leopards, while the coefficient on vagrant dogs culled remained negative and significant at $p \leq 0.10$. The marginal effects of culling were slightly different in model 3 than in model 1 and the direction of change was not systematic. The impact of culling a caracal fell from a 7.4% increase to a 5.7% increase in the probability of losses, while for leopards the marginal effect of 16% in model 1 became 27% in model 3. For vagrant dog culling the 8.3% decrease in the probability of losses at the margin became a 9.5% decrease in the probability of losses. The coefficient on other animals culled went from insignificant in model 1 to significant at $p \leq 0.10$ in model 3. The negative sign on other animals culled in model 3 is problematic as it suggested that other, untargeted culling reduces subsequent livestock losses.

The signs and significance of trapper effort and distance from town from model 1 were confirmed in model 3. At the margin the impact of an additional visit decreased from 1.1% increase to a 0.9% increase, while the marginal effect of an extra kilometre decreased from a 0.4% increase to a 0.3% increase in the probability of losses. The rainfall results improved in model 3 compared to model 2 insofar as lagged rainfall became significant $p \leq 0.10$ in model 3. The marginal effect of the current year's rainfall increased from a 1.2% decrease in the likelihood of losses to a 1.3% decrease in the likelihood of losses. The marginal effects of rainfall in years $t-1$ and $t-2$ were opposite and of similar magnitude; in year $t-1$ an extra millimetre of rainfall would translate into a 0.6% decrease in the likelihood of losses and in year $t-2$ the same marginal millimetre of rainfall would imply a 0.8% increase in the probability of livestock losses.

The square terms were all significant and of the opposite sign as the level terms, indicating the impact of rainfall slowing down at rainfall levels further away from the mean.

Discussion

This paper set out to investigate the effects of predator culling on subsequent livestock losses. We found caracal and leopard culling to increase losses, while vagrant dog culling and other wildlife culling decreased losses. Caracal's and leopard's positive demographic compensation to culling confirms ecological expectations (Knowlton, 1972; Crabtree, 1997; Knowlton et al., 1999; Sacks et al., 1999) and improves on the findings of Conner et al. (1989) and Conradie et al. (2012), which failed to establish a link between culling and subsequent livestock losses. The result was robust to specification.

The marginal effect of culling a leopard was enormous. Results indicated a 27% increase in the probability of a farm experiencing livestock losses after culling a leopard, compared to what it might have been otherwise; the effect was five times as large as the marginal effect of culling a caracal. Given the lack of other similar estimates, we do not know what these results mean or how they might vary with season, terrain and management practices. It is possible that the two estimates merely reflect difference in the prevalence of caracal and leopard culling, but there could well be more to this finding. It is equally possible for demographic compensation to be systematically larger in apex species than in minor predators, of which total population is limited by apex predator numbers.

Surprisingly, we found more trapper effort to systematically worsen livestock losses when controlling for the amount of animals culled, which as far as we know has not been documented before. This finding is hard to explain as it flies in the face of the assumption that human presence in the ecosystem acts as a deterrent to predation. The only explanation we could surmise was that damage resulted from predators that might have reclaimed former ranges from which they were chased during the previous season.

The lack of significance of the lagged losses variable in models 1 and 3 means that the culling efficiency models were preferred to ecological dynamics model (model 2) where the significance of the lagged losses variable pointed to unobserved farm characteristics systematically affecting livestock losses. However, given the all the data limitations, we were surprised by the explanatory power of model 2. The extent to which rainfall in year $t-1$ determines primary plant productivity in year t is the extent to which we confirmed the Sacks and Neale (2007) finding that livestock losses in year t are inversely related to primary plant productivity in year t . In addition, we found predator population to be correlated with livestock losses over a two-year period, indicating potentially more complex trophic dynamics than those modelled in Sacks and Neale (2007).

Several serious data limitations prevent these results from being entirely conclusive. The first, and perhaps most serious, was the implicit assumption that predator territories coincide with farm boundaries, something which is almost certainly not true. Truly modelling culling effectiveness at the farm-level will only become possible once we have farm-level data on prey and predator dynamics. Second, we had to make heroic assumptions about trophic dynamics and omit livestock husbandry factors altogether, whilst both issues are widely acknowledged to affect livestock losses (Robel et al., 1981; Knowlton et al., 1999; Sacks and Neale, 2007; Dar et al., 2009; Thorn et al., 2012). Given the historic nature of this dataset, there was not much that could be done otherwise,

but this is likely to affect the estimated compensation rates. Finally, it is key to have better spatial information not just about prey and predator populations, but also about culling effort. Farmers will remain sceptical of any compensation result which derives from spot treatments, which are well known not to work as predator control strategy (Gese et al., 1989; Knowlton et al., 1999). According to farmers, the real test is whether demographic compensation still occurs in the presence of a large, area-wide blanket control programme.

Conclusion

This study investigated the effectiveness of predator culling as protection against livestock losses. It found culling to systematically increase subsequent livestock losses when controlling for trophic dynamics, culling effort and remoteness. While the management implications of these results seem obvious, farmers stand to lose a great deal to predators and are therefore likely to remain sceptical of no-cull recommendations. This makes it important to continue studying the effects of culling in different contexts, especially where management and environmental data can be combined to do so.

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