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The Effect of Predator Culling on Livestock Losses: Caracal Control in Cooper Hunting Club, 1976 – 1981

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Abstract

This paper investigates the effectiveness of predator culling as a means of reducing livestock losses using hunting club data for Cooper (outside Mossel Bay) for the period 1976 to 1981. Results showed that caracal (Caracal caracal) culling increased subsequent livestock losses when compared to farms where fewer caracals were culled. When controlling for lagged rainfall, remoteness and a proxy for other unobserved farm characteristics, a logit model indicated the marginal effect of culling to be a 17.5% increase in the likelihood of livestock losses during the next year. The corresponding negative binomial model estimated the effect of an additional caracal culled to be a 0.373 unit increase in the number of sheep lost. A lagged rainfall variable was negative and significant in both models. According to the logit results, the marginal millimetre of rain reduced subsequent losses by 1.1%. For the negative binomial model, the marginal effect of rainfall was reduced losses by 0.047 of a sheep, which was about a 5% increase in losses. The average number of livestock lost was 0.94 sheep per farm per year. Distance travelled, used to proxy remoteness, was positive in the negative binomial model and non-significant in the logit model. Lagged livestock losses were not significant in either model. This result is important because it provides support for stricter predator control regulations by showing that livestock farmers are inadvertently harming their own interests through inappropriate culling, a practice which continues to this day.

Introduction

Extensive livestock operations are characterised by slim profit margins, which are easily eroded by predator damage (Knowlton et al., 1999). In South Africa, livestock losses to predators are substantial and rising, making predator management one of the key economic threats to the industry. Van Niekerk (2010) recently estimated predators to cost livestock producers some R1.4 billion per annum, a figure which amounts to 30% of industry turnover, while Deacon (2010) recorded escalating predator problems in the Free State despite years of control.

Culling programmes' apparent inability to resolve predator problems has attracted significant attention in the carnivore ecology literature (Knowlton et al., 1999; Sacks et al., 1999; Mitchell et al., 2004). For example, in a letter to interested parties, the head of scientific services at Yellowstone National Park listed one mechanism after another whereby predator populations compensate for culling (Crabtree, 1997). These mechanisms include larger litter sizes, younger first breeding ages, higher proportions of non-dominant adults breeding, sex ratios skewed towards females and better pup survival. Closer to home, Bingham and Purchase (2002) documented fast population recovery in black-backed jackal (*Canis mesomelas*) populations, while Marker and Dickman (2005) noted caracals' (*Caracal caracal*) ability to recolonise a vacant territory over large distances. These findings raise a serious question about the effectiveness of culling programmes as livestock protection strategies.

In South Africa, the status quo is that state-supported culling programmes have been abandoned. Recent upsurges in livestock losses have made farmers question the wisdom of this policy. In several cases previously state-supported hunting clubs have been resurrected as private operations to which neighbours contribute funds proportional to the number of black-backed jackals (*Canis mesomelas*) or caracals (*Caracal caracal*) killed on their land. These actions have effectively reopened the debate on the desirability and effectiveness of predator culling programmes. This paper investigates the question using hunting club data for Cooper in the Southern Cape, where the farming system is characterised by a mix of wool sheep and grain production.

Conner et al. (1998) presented one of the first quantitative models to investigate culling effectiveness. Using data from a 2,170 hectare sheep research station in California, these authors found livestock losses to explain variations in hunting effort, and hunting effort in turn to explain culling success, but they failed to show that culling had any impact on the next year's livestock losses. Running similar models on hunting club data for Ceres from the late 1970s, Conradie

(2012) also failed to find a significant relationship between culling and subsequent losses at the farm level. This means that despite the strong ecological assumptions about the negative impacts of culling, the issue of culling effectiveness is still an open question, and it is the key focus of the analysis which follows here. We used farm-level data from the Cooper hunting club, which operated outside Mossel Bay in the late 1970s, to run a culling effectiveness model based on Conner et al.'s (1998) work. In the literature, logit (Dar et al., 2009) and negative binomial regressions (Thorn et al., 2012) have been used to model livestock losses, but as far as we know these two functional forms have not yet been compared directly, using the same model specification and data.

A description of the available data and the model specification are presented in Section 2. Results follow in Section 3, with a discussion of these results in Section 4. The paper ends with brief conclusions.

Methodology

Study Area and Data Availability

The map in Figure 1 indicates the location of the study area. It shows Cooper to straddle the Gouritz River, but the majority of sample farms to have been on the Mossel Bay side of the river. The area's terrain caused ongoing predator problems for farmers. Mixed farming systems in the area combined dryland grain production on the uplands with irrigated agriculture on river bottoms. The steep riverbanks remained covered in dense natural vegetation, making them perfect highways for wildlife to follow down from the wilderness areas of the Cape Fold Mountains to the north. According to the 1981 farm census, the average sheep holdings for Riversdale and Mossel Bay were 450 and 380 breeding ewes respectively. In the early 1980s, farm sizes were a modest 600 to 700 hectares, and the average sheep holdings for Riversdale and Mossel Bay were 450 and 380 breeding ewes respectively (Statistics South Africa, 1981). In addition to sheep and grain, the area produced thatch reed (*Thamnochortis insignis*), *Aloe ferrox* sap, fynbos wildflowers, dairy products and honey (Horn, 2006).
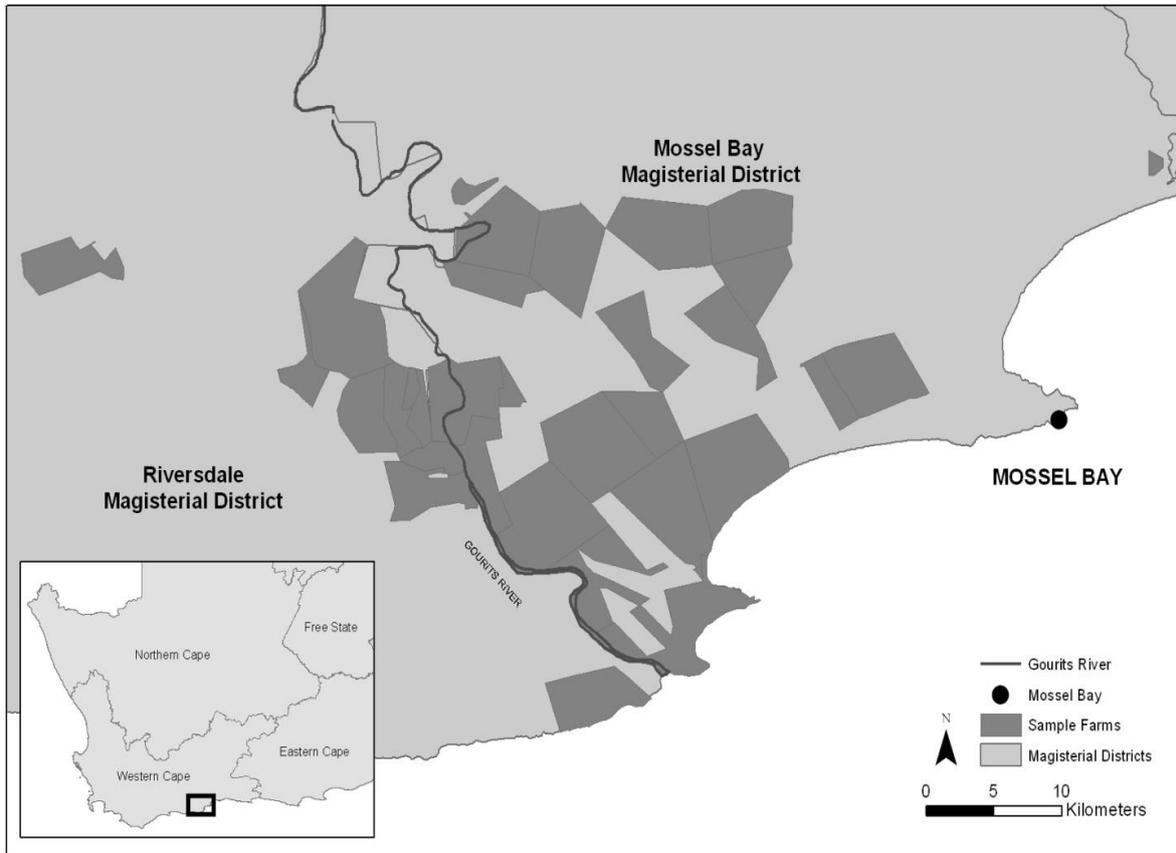
Figure 1: Map of Cooper hunting club's area

The dataset used to model the effect of culling on livestock losses came from the Cooper Hunting Club's logbooks. We had data for the period October 1976 to September 1981, when Mr CJ Honiball was employed as the club's full time hunter. The dataset includes observations for 43 farms, the majority of which experienced a stock loss event at least once during the period covered. The logbooks contained daily handwritten entries, each of which detailed the destination of and reason for each visit, the number of livestock lost and predators culled, if any, and the trip distance.

Daily records were captured in a spreadsheet where they were aggregated up to a year. Unique combinations of farm and contact names were treated as separate observations. The number of sheep, lambs and goats lost were added up to construct a stock losses variable, which was used as dependent variable in the regressions. Unlike the meticulous records of the Ceres hunting club (Conradie, 2012), the information provided in the Cooper records was rather unclear and sometimes downright incomplete. This made it difficult to always link a stock loss incident to a particular cause, and therefore it was impossible to exclude hunting effort spent on controlling poultry losses or crop losses from the dataset.

Specification of the Culling Effectiveness Model

We drew on the literature for a list of explanatory variables. The most important explanatory variable was the one capturing the culling effect. In Conner et al. (1998) this variable was a straightforward number of coyotes (*Canis latrans*) culled during a twelve-month period. Again using a twelve-month period, Conradie (2012) estimated separate culling models for leopards (*Panthera pardus*), caracals and vagrant dogs (*Canis familiaris*), as well as a model in which livestock losses were related to aggregate culling. Table 1 clearly identifies caracals to have been the main problem in Cooper in the early 1980s, but we also wanted to account for other culling. We experimented with aggregate culling variables for animals which were considered predators of sheep, for example African wild cat (*Felis libyca*), black-black jackals (*Canis mesomelas*), leopards and vagrant dogs, and all other animals including honey badgers (*Mellivora capensis),* porcupines (*Hystrix africaeaustralis*) and baboons (*Papio ursinus*), but we found the idea unviable due to inadequate sample size. Instead we added up all animals culled, excepting caracals. The coefficient on this variable would capture the effect of untargeted culling. If the ecologists are right, the expected sign on the culling variables would be positive and significant. If, on the other hand, farmers are right about the benefits of culling, the coefficient on caracals culled (and perhaps all other animals culled) would be negative and significant. Failing to establish significance, neither Conner et al. (1998) nor Conradie (2012) have been able to resolve this question.

The common determinants of livestock predation include flock size, isolation of the farm, terrain, husbandry practices, including lambing season and herding, and seasonal effects. Livestock losses have been found to be positively correlated with flock size (Robel et al., 1981; Marker and Dickman, 2005; Michalski et al., 2006; Sangay and Vernes, 2008; Hemson et al., 2009). Livestock losses have been shown to be negatively correlated with proximity to human settlements and positively correlated with distance from protected areas (Robel et al., 1981; Woodroffe, 2000; Michalski et al., 2006; Schiess-Meier et al., 2007; Sangay and Vernes, 2008; Inskip and Zimmermann, 2009; Gusset et al., 2009), perhaps merely reflecting the variation in relative density of predator populations. There is a large literature on factors which influence the impact of livestock protection measures. Studies conducted in Kansas and Botswana found that farmers who confined their livestock at night suffered fewer losses than those who did not (Robel et al., 1981; Gusset et al., 2009). Herding and fencing were shown to be beneficial (Graham et al. 2005; Kolowski and Holenkamp, 2006; Gusset et al., 2009; Hemson et al., 2009), while some authors have recommended attempts to desynchronise lambing and predator whelping seasons (Robel et al., 1981; Michalski et al., 2006; Thorn et al., 2012).

Unfortunately, our dataset was not detailed enough to operationalise most of the predicted relationships between culling and subsequent livestock losses found in the literature. The logbooks contained no information about husbandry practices, farm size or the size of livestock holdings, therefore none of these relationships could be modelled. The best we could do with respect to terrain was to use the distance between the hunter's base of operations and a given farm as an indication of that farm's remoteness. We expected a positive relationship between stock losses and remoteness; in other words, we expected more remote farms to be more susceptible to depredation than less remote farms (Robel et al., 1981; Woodroffe, 2000; Michalski et al., 2006; Schiess-Meier et al., 2007; Sangay and Vernes, 2008; Inskip and Zimmermann, 2009; Gusset et al., 2009).

While seasonal variation in livestock losses is well documented (Patterson et al., 2004; Kolowski and Holekamp, 2006; Schiess-Meier et al., 2007; Sacks and Neale, 2007), it is unclear exactly what is the relationship between rainfall and predation. Patterson et al. (2004) recorded more losses in a wet year and explained this phenomenon as natural prey becoming harder to find when it rains all the time. On the other hand, Sacks and Neale (2007) reported more livestock losses in a dry year. For modelling prey-predator dynamics, we had to resort to a spatially invariant rainfall variable obtained from the South African Weather Service. Following Sacks and Neale (2007), we interpreted the current season's rainfall as an indication of primary plant productivity and hypothesized a negative relationship between it and stock losses. Since we were already lagging the culling variable, it seemed a good opportunity to simultaneously test the Sacks and Neale (2007) lagged rainfall hypothesis. These authors suggested a good rainfall year to lead to a prey build-up, which in turn would lead to an increase in predator density, ceteris paribus causing higher livestock losses the next year.

The number of visits per year was used as a proxy for hunting effort, but instead of running a separate regression to explain level of culling with hunting effort as did Sacks and Neale (2007) and Conradie (2012), we controlled for hunting effort in the culling effectiveness regression. Squared terms were introduced to check for non-linear effects. Finally, a lagged stock loss variable was introduced to capture unobserved farm characteristics. The full specification of our culling effectiveness model for Cooper was as follows:

$$
\begin{aligned}
Stock\ losses_t = {} & a_0 + a_1 caracal\ culled_{t-1} + a_2 (caracal\ culled)_{t-1}^2 + a_3 other\ culled_{t-1} \\
& + a_4 (other\ culled)_{t-1}^2 + a_5\ distance_t + a_6 (distance)_t^2 + a_7 rain_t + a_8 (rain)_t^2 \quad [1] \\
& + a_9 rain_{t-1} + a_{10} (rain)_{t-1}^2 + a_{11} visits_{t-1} + a_{12} (visits)_{t-1}^2 + a_{13}\ stock\ losses_{t-1} + \varepsilon
\end{aligned}
$$

Functional Form

If livestock losses are viewed as a dichotomous outcome, where a farm either did or did not experience losses in a given year, a logit regression is appropriate:

$$\log\left(\frac{p_{it}}{1-p_{it}}\right) = X\beta_i + u_{it} \qquad [2]$$

where p_{it}= probability of experiencing livestock losses on a given farm in a given year. In this formulation, the regression coefficients could be transformed to measure the marginal effect of a one unit change in an independent variable on the probability of experiencing stock losses. Alternatively, livestock losses can be thought of as a count variable which follows a Poisson type distribution. To be Poisson:

$$Y_{it} = E(Y_{it}) + u_{it} = \mu_i + u_{it} \qquad [3]$$

where Y_{it} is an independently distributed Poisson random variable with mean μ_i for each individual expressed as:

$$\mu_{it} = E(Y_{it}) = X\beta + u_{it} \qquad [4]$$

The usefulness of the Poisson regression is severely restricted by the assumption of mean equals to variance (Gardner et al., 1995). Where there is overdispersion, either because some unobserved variable in the data causes some units to have higher counts than others, or because the assumption of independent observations is violated, the negative binomial regression is more suitable than a Poisson regression since it does not assume independence and can explicitly model the degree of overdispersion (Gardner et al., 1995; Gujarati, 2003). Allowing for heterogeneity in the conditional mean of the Poisson model with ε_{it} one gets (Greene, 2008):

$$Y_{it} = E(Y_{it}) + \varepsilon + u_{it} = \mu_i + \varepsilon + u_{it} \qquad [5]$$

with

$$\mu_{it} = E(Y_{it}) = X\beta + \varepsilon + u_{it} \qquad [6]$$

Our initial model specification was done in Stata10 using a pooled dataset and a Huber-White sandwich estimator to account for heteroskedasticity (Baum, 2006). During the testing, down procedure variables with z-values greater than one were retained. Once the model was finalised, it was re-run as Poisson and negative binomial regressions to compare the fit across regression types. We chose the best of the candidate models based on the log-likelihood value of the

final iteration and Akaike's information criterion values. When comparing two models using the same data, the model which produces the smallest value on Akaike's information criterion is considered best (Sakamoto and Kitagawa, 1987).

To account for unusually low stock losses and levels of culling in the beginning of the study period, the same models were re-run, excluding data for 1976. It generated results which did not materially differ from the results presented here.

Results

The Nature of the Human-Wildlife Conflict in Cooper Area

Human-wildlife conflict in the Cooper area in the late 1970s can be described as primarily a caracal problem. According to Table 1, 226 livestock units were lost on 43 farms between 1976 and 1981. The average loss was 0.94 sheep/lambs per farm per year and on average 26% of farms reported an incident in a given year.

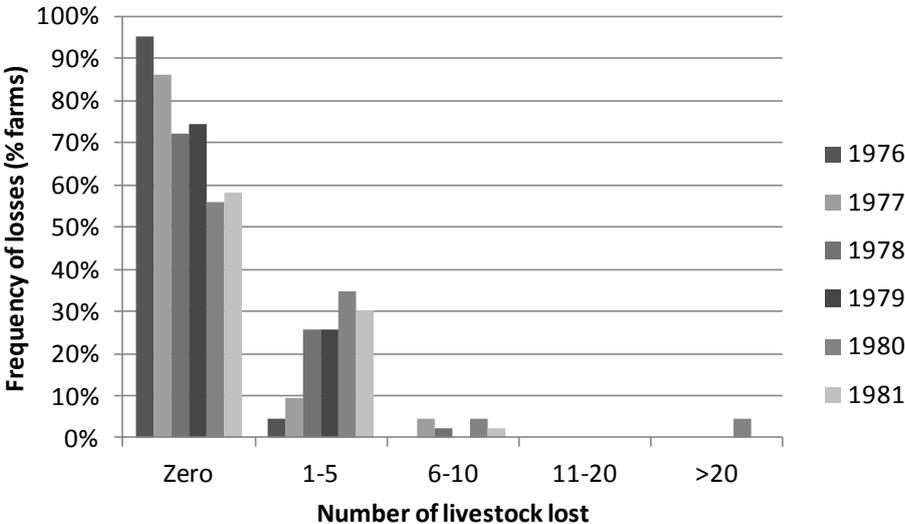*Figure 2: Frequency of reported livestock losses in the Cooper area (n=43 farms)*

Since the dataset did not contain information on the size of individual livestock holdings, we were not able to calculate the incidence rate as a proportion of livestock killed. Instead, we had to make do with an incidence rate based on the proportion of farms that reported stock losses. According to Figure 2, the

proportion of farms reporting losses increased steadily from 5% in 1976 to 42% in 1981. However, the majority of farms which suffered losses reported minor incidents, usually with five or fewer sheep/lambs lost in a year. The maximum number of sheep lost was usually in the order of nine (1977) or ten (1981), but 1980 was a particularly bad year. Large losses of 21 and 24 sheep/lambs respectively were experienced on two different farms. While the problem animal was not recorded for these two incidents, data from Ceres suggested that such large losses could have been the result of vagrant dog attacks or even stock theft (Conradie, 2012).

Table 1: Livestock losses and numbers of wildlife culled by year in the Cooper area (n=43 farms)

Type	1976	1977	1978	1979	1980	1981	Total for study period
Total livestock lost	2	22	33	31	98	40	226
Caracals	2	17	19	18	35	21	112
Black-backed jackals	0	0	0	2	4	5	11
Vagrant dogs	0	1	0	0	1	2	4
Groukatte/dikkopkatte	0	1	1	1	2	0	5
Honey badgers	0	0	3	1	2	2	8
Porcupines	0	6	5	2	3	0	16
Baboons	0	0	0	0	1	0	1
Total wildlife culled	2	25	28	24	48	30	157

Between 1976 and 1981, 112 caracals, 11 black-backed jackals and four vagrant dogs were culled on the same farms. About 18 to 20 caracals were culled every year, except for 1976 when there were virtually no problems and 1980 when 35 caracals were culled in response to large livestock loss incidents. There were also five minor feline predators culled, which were variously logged as "*groukatte*" or "*dikkopkatte*". While we are fairly certain that *groukatte* refers to African wildcat (*Felis libyca*), we are less certain of what *dikkopkatte* might have been; but given the morphology of African wildcat, we assumed *dikkopkatte* also to have been *Felis libyca*. Despite Kok (1996) reporting livestock not to form a significant part of the *Felis libyca* diet, these animals were actively prosecuted because farmers believe them to prey on newborn lambs as well as on poultry. The eight honey badgers (*Mellivora capensis)* and 16 porcupines (*Hystrix africaeaustralis*) that were reported culled during the study period were assumed to have done damage to beehives or lucerne fields.

Regression Results

Regression results are reported in Table 2. The first set of results is for a logit regression of the full specification given in equation 1. Of the hypothesized variables, only four were significant, namely the number of caracals culled ($p \leq 0.10$), the number of all other animals culled ($p \leq 0.05$), lagged rainfall ($p \leq 0.05$) and its squared term ($p \leq 0.01$). The positive sign on caracals culled was consistent with demographic compensation, while the negative sign on all other animals culled seemed to suggest other culling to provide effective protection against livestock losses. It was quite surprising to have found a negative sign on other animals culled, given that with the exception of vagrant dogs, none of the other animals culled were major predators of sheep. Although not significant at $p \leq 0.05$, the positive sign on distance was consistent with the expected positive relationship between livestock losses and remoteness. The current season's rainfall was not significant, but for lagged rainfall we found a negative and significant sign. The coefficient on hunting effort was positive and not significant.

The result of the full specification logit is followed by the final tested-down logit regression. Testing down first removed the current season's rainfall and its squared term ($p=0.825$, $p=0.809$), then visits and its squared term ($p=0.296$, $p-0.620$) and finally other animals culled and its squared term ($p=0.0.965$, $p=0.617$). The coefficients on distance and its squared term were not significant, but these variables were retained because they had z-values greater than one and because keeping them resulted in a lower Akaike value than leaving them out. The lagged livestock losses variable was kept as evidence that the unobserved farm characteristics did not significantly explain the variation in livestock losses. Comparing the log likelihood and Akaike's statistics across the full and tested-down logit specifications indicated a marginal improvement in overall fit as a result of dropping the insignificant variables.

In the final logit specification, the marginal effect of caracal culling predicted a 17.5% increase in the probability of suffering losses during the next year. The insignificant squared term indicated culling to have a constant effect. At the mean, lagged rainfall was expected to decrease the probability of livestock losses by 1.1% per marginal millimetre. The rainfall effect was expected to wash out very slowly at a rate of nine thousands of 1% per additional millimetre.

Table 2: Regression results explaining pooled count data on livestock losses$_{it}$

Variable name	Full specification logit		Final logit		Poisson		Negative binomial	
	Coefficient RSE	Marginal effect	Coefficient RSE	Marginal effect	Coefficient RSE	Marginal effect	Coefficient RSE	Marginal effect
Caracals culled$_{it-1}$	0.839*	0.164	0.887**	0.175	0.298*	0.244	0.471**	0.373
	0.476		0.347		0.163		0.192	
(Caracals culled)$^2_{it-1}$	-0.046		-0.055		-0.013		-0.037†	-0.029
	0.051		0.045		0.018		0.023	
Other culled$_{it-1}$	-1.669**	-0.327						
	0.797							
(Other culled)$^2_{it-1}$	0.084							
	0.057							
Distance$_i$	0.063		0.061		0.052		0.088*	0.070
	0.056		0.053		0.043		0.048	
(Distance)^2_i	-0.002		-0.002		-0.001		-0.002**	-0.001
	0.001		0.001		0.001		0.001	
Rainfall$_t$	-0.002							
	0.008							
(Rainfall)^2_t	1.38e-06							
	5.71e-06							
Rainfall$_{t-1}$	-0.054**	-0.011	-0.053***	-0.011	-0.056**	-0.046	-0.059**	-0.047
	0.025		0.021		0.023		0.024	
(Rainfall)$^2_{t-1}$	4.77e-04**	9.35e-06	4.61e-05**	9.10e-06	4.74e-05**	3.88e-05	5.14e-05**	4.07e-05
	2.22-05		1.85-05		2.06e-05		2.14e-05	
Hunter visits$_{it-1}$	0.079							
	0.078							
(Hunter visits)$^2_{it-1}$	-0.001							
	0.002							
Livestock losses$_{it-1}$	-0.061		-0.017		0.011		0.004	
	0.104		0.089		0.036		0.034	

Constant	13.57**	13.06**	14.80**	15.03**
	6.107	5.547	6.142	6.400
n	215	215	215	215
Wald LR test	$X^2(13)=38.07$ ***	$X^2(7)=35.36$ ***	$X^2(7)=50.31$ ***	$X^2(7)=33.84$ ***
McFadden's R^2	0.170	0.149	0.134	
Log likelihood	-110.08	-112.89	-406.59	-262.07
Akaike's IC	248.16	241.79	829.18	542.14
Over dispersal alpha				3.84**

*** signify p≤0.01, ** signify p≤0.05, * signify p≤0.10, † signify p≤0.

Re-running the final logit model as Poisson and negative binomial regressions produced similar results, although judged on the log likelihood statistic and Akaike's information criterion results, the two logit models were preferred to the Poisson and negative binomial regressions by some margin. Akaike's values were AIC = 248.16 for the full specification and AIC = 242.79 for the final logit model. At AIC = 829.18 and AIC = 542.07 Akaike's value was almost four times as high for the Poisson and twice as high for the negative binomial model. With alpha =3.84 and significantly different from zero at p≤0.000, there was evidence of overdispersal which made the negative binomial regression preferable to a Poisson model. The negative binomial regression also had a higher log likelihood statistic than the Poisson regression.

While the Poisson result could therefore be safely ignored, there was some merit in the negative binomial results despite their producing a weaker overall fit than the logit specification. For example, the coefficient on the squared term of caracals culled was marginally significant (p=0.114), as were the coefficients on distance (p=0.066) and distance squared (p=0.027). The coefficient on lagged livestock losses remained firmly insignificant (p=0.908). The marginal effect of caracal culling in the negative binomial model was to increase expected livestock losses by 0.373 of a sheep/lamb per additional caracal culled, an increase of 40% in mean losses per farm per year. The number of livestock losses increased with greater remoteness, at a rate of 0.07 sheep/lambs per farm per year for each additional kilometre travelled to the farm. The remoteness effect decreased at a rate of 0.001 sheep/lambs lost per marginal kilometre travelled. The marginal effect of rainfall meant that for every millimetre of rain above the mean, livestock losses were expected to decrease by 0.059 sheep/lambs per farm per year.

Discussion

We found caracal culling to increase the next year's livestock losses at the farm level regardless of specification or functional form. Our result was not only consistent with the ecological expectation of demographic compensation (Crabtree, 1997), but it was also in line with the experience of American culling programmes (Berger, 2006). This finding improves on previous work, which failed to estimate a significant relationship between the amount of culling and subsequent livestock losses (Conner et al., 1989; Conradie, 2012) and as far as we know, it is the first of its kind for the Southern Cape.

Given the different ways in which the dependent variable was defined in the logit and negative binomial models, the marginal effect of caracal culling could not be compared directly across the two functional forms. However, in both cases the impact was larger than anticipated. According to the logit models, marginal caracal culling increases the probability of losses by about 16% to 18%, which given the 26% average incidence of losses, represents a 40% increase in the average incidence of losses. The estimate produced by the negative binomial model was quite similar. It predicted a 0.37 unit increase in losses, which given the average loss of 0.94 sheep per farm per year, also meant a 40% increase in losses for every additional caracal culled. At the moment there is very little with which to compare these estimates; more work of this kind would be quite useful to determine if caracal culling is equally harmful under all conditions.

The attempt to account for other, and also untargeted, culling was not successful in this analysis, mainly due to a lack of observations. Therefore, the ecological hypothesis that disturbance is generally as harmful as targeted culling could not be confirmed or rejected here.

Given the severe limitations of the dataset and the extremely rudimentary nature of the environmental variables included in the culling effectiveness model, overall these variables worked surprisingly well. While it confirms that the modelling direction taken by Sacks and Neale (2007) represents a productive new avenue of enquiry, better data are needed to produce firm estimates of how livestock losses vary with trophic dynamics. The only trophic dynamics result worth commenting on is the negative and significant relationship obtained between livestock losses and lagged rainfall. We interpreted this to suggest the possibility of more complex adjustment processes than the simple twelve-month lag between predator build-up and prey build-up as described in Sacks and Neale (2007).

It is relatively easy to understand why culling did not work in Cooper in the late 1970s and why it would be unlikely to work now, even if efforts could be properly coordinated and targeted. Firstly, the map in Figure 1 clearly shows a programme of spot treatments, a tactic which is well known not to work. Attempts at population suppression on a 2,000 ha property are futile (Conner et al., 1998) and for spot treatments to work, they have to be quite intensive (Gese et al., 1989; Knowlton, 1999; Bingham and Purchase, 2002). When predators are culled, vacant territories are repopulated by dispersing juveniles, who fight fiercely and breed rapidly in an attempt to gain a territorial foothold. The resulting predator densities then could easily be higher than before the damage-causing alpha pair was removed. The second reason why culling failed is Cooper's terrain - dense riverine vegetation of the Gouritz River providing

cover and an easy access route to the wilderness areas of the Cape Fold Mountains. This means that even if predators could be controlled locally, there would always be a mechanism for long-distance dispersal, a well known characteristic of caracals (Marker and Dickman, 2005).

It is, therefore, clearly worthwhile to ask what Cooper's farmers might do to avoid livestock losses instead of culling. Increased vigilance on the behalf of farmers is a popular recommendation (Robel et al., 1981; Knowlton, 1999; Treves and Karanth, 2004; Mitchell et al., 2004), but according to Blejwas et al. (2002), targeted culling is a better solution than no culling. This persistent and problematic debate makes it even more important to understand what culling's impacts are under a variety of circumstances.

Conclusion

This study investigated the effectiveness of predator culling as protection against livestock losses in an area where the human wildlife conflict was characterised by substantial caracal damage to sheep. We found caracal culling to significantly increase livestock losses at the farm level, but all other culling not to have had an impact on losses. The estimated marginal effects of caracal culling were surprisingly large, which makes it urgent to produce comparative estimates. Since this compensatory breeding result could possibly derive from recolonisation following spot treatments, it is important that future work combines an investigation of culling effectiveness with as much spatial information as possible.

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