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RESEARCH ARTICLE

Culling recolonizing mesopredators increases livestock losses: Evidence from the South African Karoo

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Abstract Populations of adaptable mesopredators are expanding globally where passive rewilding and natural recolonization are taking place, increasing the risk of conflict with remaining livestock farmers. We analysed data from two social surveys of farmers in the Karoo, South Africa, where black-backed jackals (*Canis mesomelas*) and caracals (*Caracal caracal*) have re-emerged as a threat to sheep farms in the context of falling agricultural employment and the expansion of natural areas. We show that irrespective of measurement approach, lethal control of mesopredators in this fragmented socio-economic landscape was associated with increased livestock losses the following year. Terrain ruggedness was positively, and number of farmworkers negatively, associated with livestock losses. Our study provides further evidence that lethal control of mesopredators in this context is probably counter-productive and supports calls to develop, share and financially support a range of non-lethal methods to protect livestock, especially where natural recolonization of mesopredators is occurring. A graphical abstract can be found in Electronic supplementary material.

Keywords Black-backed jackal · Caracal · Human–wildlife conflict · Lethal control · Mesopredators · Small-livestock farming

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13280-019-01260-4) contains supplementary material, which is available to authorized users.

INTRODUCTION

Agricultural land abandonment in Europe (Breustedt and Glauben 2007; Renwick et al. 2013) and in North America (Brown et al. 2005), coupled in many places with 'passive rewilding' in the form of expanding scrubland, forested and protected areas (Navarro and Pereira 2015), has created opportunities for predators, and especially mesopredators such as coyote (*Canis latrans*), golden jackal (*Canis aureus*) and crab-eating foxes (*Cerdocyon thous*), to recolonise or expand their distribution range (Gompper 2002; Laliberté and Ripple 2004; Larue et al. 2012; Trouwborst et al. 2015; Milanesi et al. 2017; Somsen and Trouwborst 2019). Where this has resulted in concern about actual or potential livestock losses, such recolonisation has contributed to conflict with remaining livestock farmers (Smith et al. 2014; Álvares et al. 2018). The long-standing debate over whether lethal predator control is successful in preventing the decline in the small-livestock industry has re-emerged in this new context (Berger 2006; Treves et al. 2016; Bergstrom 2017).

The South African experience may offer insights in this regard. Many sheep farmers in the dry interior Karoo are in conflict with two mesopredators (Figs. 1 and 2): the black-backed jackal (*Canis mesomelas*), henceforth jackals, and to a lesser extent the caracal (*Caracal caracal*). The conflict with jackals has been a new experience for most sheep farmers. During the twentieth century, farmers were provided with substantial government support to combat predation in the form of bounty payments, subsidised fencing, provision of poison and support for hunting with dog packs. Such policies enabled them to exclude jackals from fenced camps fed by artificial water sources and to limit predation by caracals (Beinart 2003; Nattrass et al. 2017). However, by the transition to democracy in 1994, the

Fig. 1 Black-backed jackal (*Canis mesomelas*) in the Central Karoo, South Africa © Nathalie Houdin & Denis Palanque, Lenses for Conservation

Fig. 2 Caracal (*Caracal caracal*) in the Central Karoo, South Africa © Nathalie Houdin & Denis Palanque, Lenses for Conservation

political power of sheep farmers had waned substantially, and the institutional context was very different. Starting in the early 1980s, liberalisation of agricultural policy put an end to most subsidies and changing wildlife management strategies first removed support for lethal control of predators and then restricted the use of poison. These changes, together with falling agricultural employment, land use change—including the growth of 'life-style' (non-commercial) farming (Reed and Kleynhans 2010; Conradie et al. in press) and the growth of protected areas—enabled jackals to recolonise Karoo sheep farms, risking the economic viability of many of them (Carruthers and Nattrass 2018; Drouilly et al. 2018c). According to the first surveys of the economic impact of predation in South Africa, losses to predators amounted to an estimated 10 to 30% of wool and mutton industry turnover (van Niekerk 2010; Conradie and Nattrass 2017). Most were blamed on the jackal.

Two rival 'narratives' emerged in response: a scientific 'ecological' narrative favoured by conservationists and biologists; and a 'farmer' narrative in support of lethal control (Nattrass and Conradie 2015). The ecological narrative drew on predator ecology to warn that killing territorial predators can make problems worse for farmers by releasing wild herbivore populations (thereby creating competition for grazing), disrupting predator social systems (thereby enabling younger females to breed) and facilitating compensatory immigration, potentially worsening the level of livestock depredation (Doherty and Ritchie 2017). This view has been supported by South African biological evidence suggesting that jackals are younger and have larger litters on farms, where they are heavily persecuted, than in nature reserves (Minnie et al. 2016), and that heterogeneous anthropogenic mortality induced source–sink dynamics via compensatory immigration (Minnie et al. 2018). Farmers, however, pointed out that lethal control worked in the past and that as predator numbers are a positive function of food supply, co-existing with predators on extensive livestock farms is not a stable or sustainable solution (Nattrass and Conradie 2015, Nattrass et al. 2017, in press). They worried that their extensive sheep farms provided sufficiently large quantities of easily available food that jackals would tolerate other jackals in their territory—as is the case on the Namibian Skeleton Coast with regard to seal carcasses (Jenner et al. 2011).

The South African contestation echoes a long-standing global debate over the relative benefits to livestock farmers of lethal versus non-lethal strategies, a debate plagued by reliance on different types of evidence and research strategies (Treves et al. 2016; Doherty and Ritchie 2017). The South African farmer narrative is supported by research linking jackal litter size to food availability (Moehlman 1987; Bingham and Purchase 2002) and by the historical record showing that given sufficient resources, lethal control and fencing were effective in excluding jackals from Karoo sheep farms (Beinart 2003; Nattrass et al. in press; Carruthers and Nattrass 2018). Yet, the Karoo has undergone significant changes in social relations and political power (Hill and Nel 2018; Walker et al. 2018) since the mid-20th century and the kind of orchestrated campaign against predators that pushed jackals off sheep farms in the mid-twentieth century is unlikely to be replicated. The relevant question today is whether lethal control, in the current context of fragmented social and economic Karoo landscapes, reduces or exacerbates the predation problem on sheep farms.

Treves et al. (2016) argue that random assignment or quasi-experimental case control is essential if scientifically acceptable inference is to be drawn about the relative effectiveness of lethal versus non-lethal control. We agree that such methods can be helpful, but suggest that other forms of evidence, such as historical data and longitudinal social surveys amongst farmers can be complementary and can help shed light on context-specific ecological dynamics and adaptations on the part of both farmers and predators. For example, in the United States, Berger (2006) used historical data over the period 1920–1998 to argue that lethal control of coyotes had been ineffective in reducing predation losses and that other factors had been more important. In South Africa, Conradie and Piesse (2013) used hunting club data from the 1980s and found that farms where caracals were hunted experienced worsening problems over time, suggesting that lethal control may have been counter-productive.

A later longitudinal social survey of Central Karoo sheep farmers by Conradie collected detailed farm-level information, including predator control and livestock losses between 2012 and 2014. Using Conner et al.'s methodology of regressing the number of coyotes killed in the previous period on current livestock losses (Conner et al. 1998), analysis of this data revealed that a 10% increase in culling predators the previous year was associated with a 5.6% increase in reported stock losses the following year—a finding that was robust to the inclusion of controls for year as well as socio-economic and farm-level characteristics (Nattrass and Conradie 2018).

This paper draws on the Conradie longitudinal survey data as well as data from a further study of Karoo sheep farmers to test whether different approaches to measuring livestock losses and the inclusion of geographical controls affect the positive relationship between lagged predators culled and livestock losses. Following Drouilly et al. (2018c), we hypothesised that terrain ruggedness would be positively correlated to small-livestock losses as it creates cover for predators. We also include an additional geographic variable, namely distance to Anysberg Nature Reserve, the nearest protected area (PA). Internationally, it has been shown that losses often increase closer to PA (Wang and Macdonald 2006; Gusset et al. 2009) and locally, farmers argue that PAs are an important source of young dispersing jackals. We were agnostic as to whether this variable would prove to be a significant predictor of predation given that young jackals and caracals can disperse over distances greater than 100 km from their natal den (Stuart 1982; Ferguson et al. 1983; Humphries et al. 2016), implying that farms might need to be located more than 100 km away from a PA if they are going to experience any protective effects.

MATERIALS AND METHODS

The Central Karoo (longitude 22.238402, latitude—32.814620) is located < 400 km from Cape Town between the Swartberg Mountains in the south and the Great Escarpment in the north. It is a dry region (average annual rainfall of less than 150 mm per annum) with a long history of sheep farming. In 2012, Conradie approached 98 sheep farmers in the area through agricultural associations and was able to recruit 71 for her longitudinal study. Of these, 66 participated in the 2012, 2013 and 2014 surveys. She asked farmers each year about their farming practices, number of predators culled and livestock lost to predators (for more detail on the survey see Nattrass and Conradie 2018, Conradie et al. in press).

There is no universally adopted approach to measuring the predation rate and this can create difficulties in comparing studies. Some measures express lambs lost to predators as a percentage of total lambs, others express lambs lost as a percentage of the entire flock or as lambs plus adults lost to predators as a percentage of the flock (Pearson 1986; Knowlton et al. 1999; Graham et al. 2005). The measure of lambs lost itself varies depending on whether only those lambs that lived long enough to be counted ('tagged') are included in the measure (as known lambs lost), or whether an estimate of perinatal ('pre-tagging') losses is also allowed (Connolly 1991; Conradie and Nattrass 2017). Estimates of adult sheep and lambs lost post tagging—as measured in the Conradie data set—are likely to be more precise estimates of losses to predators, but to the extent that mesopredators like jackals and caracals kill new-born lambs (Drouilly et al. in press), excluding estimates of pre-tagging losses from estimates of losses to predators will inevitably understate the predation problem.

In 2014, Drouilly surveyed many of the same farmers, asking them for their estimate of lambs lost to predators. She approached farmers in the Central Karoo using word of mouth and agricultural organisations (see Drouilly et al. 2018c for more detail) and was able to recruit 77 sheep farmers, 45 of whom were already participating in Conradie's panel study. Drouilly's primary research concern was to probe local knowledge and attitudes towards wildlife and strategies to combat predation. She asked farmers about their number of breeding ewes, what percentage of these ewes had become pregnant, whether they scanned their sheep to verify pregnancy, and for the farmer's estimate of how many lambs, as a percentage of pregnant ewes, had been lost to predators. This allowed for an estimate of lambs lost to predators irrespective of whether this was pre- or post-tagging and thus had the advantage over estimates based only on losses post tagging. But it had the disadvantage of relying on the judgement and impressions of farmers about their pre-tagging losses, rather than on tagging records.

We draw on data from both surveys to compare the different strategies for estimating losses to predation and to explore the relationship between predators culled the previous year (drawn from Conradie's 2013 survey) and losses to predators in 2014. Following Nattrass and Conradie (2018), we draw on data from the Conradie survey to control for other factors likely to affect predation, notably total number of livestock (a proxy for the size of the farm), the extent to which farmers understocked their land, whether the farm had any riverine habitat and human presence on the land (number of full-time farmworkers and whether the farmer lived on the farm).

The degree of under-stocking was calculated as the difference between the actual stocking level (livestock units per hectare) and the official recommended stocking rate for the farm (determined by government inspectors and based on rainfall, plant productivity, etc.). Official recommended stocking rates exist for each farm and were provided to Conradie by the farmers. The degree to which a farm is understocked can be interpreted as the degree to which primary plant productivity is set aside for natural prey. Sacks and Neale (2007) found a negative relationship between plant productivity and livestock losses in north-coastal California (a Mediterranean ecosystem) suggesting that allowing a wild prey base (e.g. antelopes, rodents) to flourish on the land could potentially help prevent predation of sheep. We included the under-stocking rate into our model to control for such potential effects. However, under-stocking might also occur where farmers believe that the land can no longer support as many livestock as indicated by the official carrying capacity (for example, if the land has become over-grazed or if there have been extended periods of relatively low rainfall). In such cases, there will be less primary plant productivity available to support an alternative prey base for predators than indicated by the under-stocking rate.

Riverine habitat (a dummy variable indicating the presence of riverbeds and related vegetation, which offers cover for predators in this sparely vegetated landscape) was expected to be positively correlated with livestock losses and hence was included as a control variable in the regression. Human presence on the land, proxied by the number of farmworkers permanently employed on the farm in 2014, and whether the owner lived on the farm, was expected to be negatively correlated with livestock losses. Models were evaluated using a combination of overall goodness of fit ($p \leq 0.05$), the sign and significance level of important coefficients (various levels), log likelihood and Akaike and Bayes' information criteria (minimised). Inverse hyperbolic sine (IHS) transformations were used on the number of predators culled, livestock numbers and losses to predators in order to normalise the distribution for these variables.

We run these regressions on both the Conradie estimate of livestock losses to predators (which included only those lambs lost post tagging) and the Drouilly measure (lambs lost pre- and post-tagging). Then we run the same model on a composite measure of losses to predators calculated as the average of the two estimates and then extend that model to include the geographic variables.

In earlier research, Drouilly et al. (2018c), using the Drouilly data set, showed that terrain ruggedness was a statistically significant predictor of whether farmers believed jackal, caracal and chacma baboons (*Papio ursinus*) posed a serious risk to their farm. Terrain ruggedness provides cover for stalking predators (Avenant et al. 2016) and protection against human persecution. We include an indicator of ruggedness using GDAL's Terrain Ruggedness Index (TRI) function (from within QGIS) which implements Wilson et al.'s (2007) TRI measure. This TRI is defined as the mean absolute difference between the elevation of a central square of land and its eight surrounding similarly sized squares of land. The elevation data used was Shuttle Radar Topography Mission (SRTM) 1 Arc-Second Global (USGS 2018) hence each similarly sized square of land measured 30 m by 30 m. The TRI thus gives an indicator of changes in elevation over a relatively small area. The TRI for each main farm would consist of many thousands of cells, the mean of which produces the farm-level index of ruggedness.

We extend the geographic analysis further by including another variable, 'distance from Anysberg' that was obtained by measuring the Euclidean distance between the closest pair of edges between the PA and each main farm. The geographical variables were created in QGIS (QGIS Development Team 2018) using GIS data for the main farms in the joint data set. The data were analysed in Stata version 15.1.

RESULTS

Figure 3 plots the estimated losses to predators for the 45 farmers who provided data to both Drouilly and Conradie.

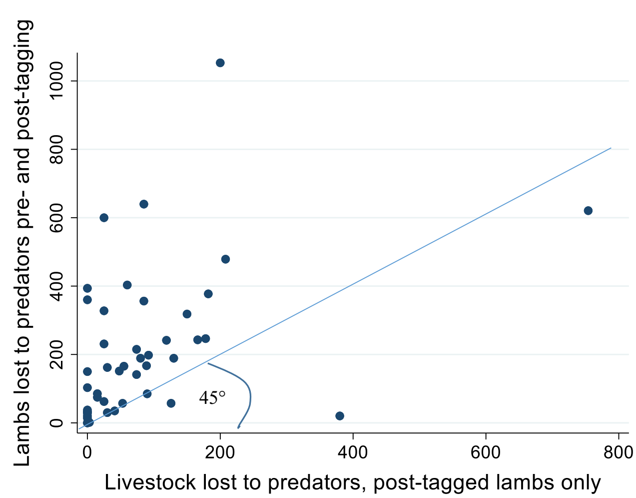

Fig. 3 Comparing the two measures of livestock lost to predators

The estimates were weakly correlated (Pearson correlation coefficient = 0.43, $p \leq 0.003$). Drouilly's estimated losses were systematically higher than Conradie's even though the Conradie methodology included adults and lambs lost, whereas Drouilly focused only on lambs. This was because almost all predation involved lambs and Drouilly's methodology allowed farmers to include their estimate of pre-tagging losses. According to the Drouilly estimates, the mean estimated lambs lost to predators was 208.8 (standard deviation: 215.3), whereas the mean value for the Conradie estimate of adult sheep and tagged lambs lost was 82.5 (standard deviation: 128.5).

Figure 3 stands as an illustration of how estimated losses to predators can vary significantly across surveys, a function not only of different research and measurement strategies, but probably also other unmeasurable factors such as interviewing technique and personal/ethnic characteristics of the interviewer (Adida et al. 2016) that might affect the veracity of answers. Whether one of the estimates was somehow better, more accurate or appropriate is not the task of this paper. Our approach is rather to assume that both have strengths and weaknesses and that what is of more concern is whether these different approaches (or a combination of both) support, or fail to support, the emerging ecological narrative that killing more predators in 2012/2013 was associated with higher livestock losses in 2013/2014.

Table 1 presents our regressions on the number of livestock losses to predators using the Conradie estimate (models 1 and 2), the Drouilly estimate (models 3 and 4) and the composite measure (models 5 and 6). All show a statistically significant and substantial relationship between predators culled in 2012/2013 and losses to predators in 2013/2014—with the size effect being stronger for the Conradie estimate than the Drouilly estimate. In the univariate regression models 1 and 3, a 10% higher number of predators culled in 2012/2013 was associated with either a 7.2% or a 4.9% increase in livestock lost in 2013/2014 depending on whether the Conradie estimate (model 1) or the Drouilly estimate (model 3) was used. These size effects declined with the inclusion of control variables (models 2 and 4), as did the level of statistical significance (from the 5 to the 10% level). The signs on the control variables were in the expected direction and consistent between regressions 2 and 4. Very few of the control variables were statistically significant, and those that were had small size effects (in regression 2, having no riverine habitat reduced predicted livestock losses by 1.8 and in regression 4, every additional worker reduced predicted lambs lost by 0.2).

Regressions 5 and 6 run the models on the simple average of the Conradie and Drouilly estimates of losses to predators. The relationship between predators culled the previous year and stock losses remained strong (a 10% higher number of predators culled in 2012/2013 was associated with 5% higher losses to predators in 2013/2014) and statistically significant (dropping from the 1% level to the 5% level with the inclusion of the control variables). The test statistics suggest that the models based on the composite measure were stronger than those for the separate Conradie or Drouilly measures.

Model 7 continues the regression analysis on the composite measure of losses to predators, this time adding the two geographical variables: farm ruggedness and distance from Anysberg Nature Reserve. It shows that the greater the ruggedness index, the higher the level of reported losses. Distance from the PA has no substantial or statistically significant effect. Finally, regression 8 provides the best fitting model, which shows that controlling for total livestock, number of farmworkers, terrain ruggedness (all of which were statistically and substantively significant), a 10% higher number of predators culled in 2012/2013 was associated with 4% higher livestock losses in 2013/2014.

DISCUSSION

This paper used two different data sources and associated measures of losses to predators to show that irrespective of the estimate, the positive relationship between predators culled and livestock losses the following year remains robust—and continues to do so whilst controlling for a range of socio-economic and landscape characteristics. We found, consistent with Drouilly et al. (2018c), that more rugged farms suffered higher livestock losses. Some biological research suggests that PAs might operate as a source for dispersing jackals (Minnie et al. 2018) and many farmers believe that jackals living in PAs cross dilapidated fences to prey on sheep in neighbouring farms. However we found that distance from the local PA was neither statistically nor substantively significant in predicting livestock losses. The finding is consistent with research on jackals in Anysberg showing they subsist on natural prey and did not eat sheep (Drouilly et al. 2018a, b).

Our findings are also consistent with genetic evidence from jackals and caracals showing no significant spatial structure and no detectable barriers to their dispersal across South Africa, albeit with a small sample size (Tensen et al. 2018, 2019). Figure 4 illustrates how a subadult male jackal and a subadult female caracal were able to move quickly and over long distances across the Central Karoo. The jackal travelled across the Karoo basin, crossing 110 farms and covering over 2000 km in 4 months, providing researchers with more than 4000 GPS points in the process. His journey began 250 km north-east of Anysberg. He then travelled south-west almost all the way to Anysberg in 3

Table 1 Tobit regression on number of small-livestock lost to predators (IHS transformed)

	Livestock lost to predators, including only lambs lost post tagging		Lambs lost to predators pre- and post-tagging		Livestock lost to predators (average of the two estimates)			
	1	2	3	4	5	6	7	8
Predators culled in the previous year (IHS transformed)	0.72*	0.75#	0.49*	0.41#	0.52**	0.49*	0.46*	0.37*
	(0.36)	(0.39)	(0.18)	(0.21)	(0.17)	(0.20)	(0.18)	(0.17)
	$t = 2.01$	$t = 1.88$	$t = 2.66$	$t = 1.92$	$t = 2.98$	$t = 2.49$	$t = 2.48$	$t = 2.15$
Total number of livestock (IHS transformed)		0.66		0.63		0.47	0.67#	0.79*
		(0.72)		(0.42)		(0.38)	(0.38)	(0.33)
		$t = 0.93$		$t = 1.52$		$t = 1.23$	$t = 1.78$	$t = 2.41$
Under-stocking rate		− 0.05**		0.012		0.01	0.01	
		(0.02)		(0.01)		(0.01)	(0.01)	
		$t = -2.20$		$t = 1.25$		$t = 0.56$	$t = 1.25$	
No riverine habitat		− 1.80#		− 0.405		− 0.56	− 0.50	
		(1.03)		(0.552)		(0.51)	(0.47)	
		$t = -1.75$		$t = -0.73$		$t = -1.11$	$t = -1.06$	
Permanent farmworkers		− 0.24		− 0.210*		− 0.18#	− 0.19*	− 0.19*
		(0.19)		(0.10)		(0.10)	(0.09)	(0.09)
		$t = -0.17$		$t = -2.03$		$t = -1.93$	$t = -2.10$	$t = -2.12$
Farmer lives on farm		− 0.23		0.588		0.62	0.34	
		(0.132)		(2.749)		(0.72)	(0.68)	
		$t = -0.17$		$t = 0.75$		$t = 0.86$	$t = 0.50$	
Ruggedness index (TRI_Riley)							5.64*	4.23*
							(2.09)	(1.80)
							$t = 2.70$	$t = 2.35$
Distance from anysberg (kilometres)							0.01	
							(0.01)	
							$t = 1.04$	
Constant	0.70	− 1.66	2.70***	− 0.87	3.15***	− 0.14	− 3.76	− 3.09
	(1.32)	(4.82)	(0.60)	(2.75)	(0.63)	(2.54)	(2.71)	(2.41)
	$t = .53$	$t = -0.34$	$t = 5.41$	$t = -0.32$	$t = 5.01$	$t = -0.06$	$t = -1.39$	$t = -1.28$
N	41	41	44	41	41	41	41	41
Log likelihood	− 86.51	− 79.75	− 83.79	− 74.89	− 75.38	− 71.46	− 67.99	− 70.08
Prob > chi2	0.045	0.008	0.010	0.028	0.005	0.015	0.004	0.001
AIC	179.01	175.50	173.57	164.98	156.77	158.92	155.98	152.16
BIC	184.15	189.21	178.93	178.69	161.92	172.63	173.12	162.44

A Tobit regression is used to accommodate the small but significant numbers of those farmers who cull no predators

Figure in brackets is the standard error. ***($p < 0.001$); **($p < 0.01$); *($p < 0.05$); #($p < 0.1$)

weeks and circled back to settle on a sheep farm with no permanent human presence. The caracal travelled north of her capture site and covered more than 400 km in 3 months crossing more than 20 farms in the process. The two cases are clearly not statistically representative, yet provide an illustration of how far, and quickly, young jackals and caracals can move across the Karoo—and hence that distance from a PA like Anysberg is unlikely to provide much, if any protection, to farmers. The recently recorded journey of an arctic fox, which travelled 4415 km in 76 days similarly demonstrated that mesopredators are capable of moving far and fast when dispersing (Fuglei and Tarroux 2019).

More evidence for the rapid recolonization of the Central Karoo by jackals and caracals is obtainable from Drouilly et al. (2018c). Our social survey data together with the GPS collar data from the two subadult mesopredators and some recent genetic analyses offer potential explanations as to why the distance from Anysberg Nature Reserve did not emerge as a substantial or statistically

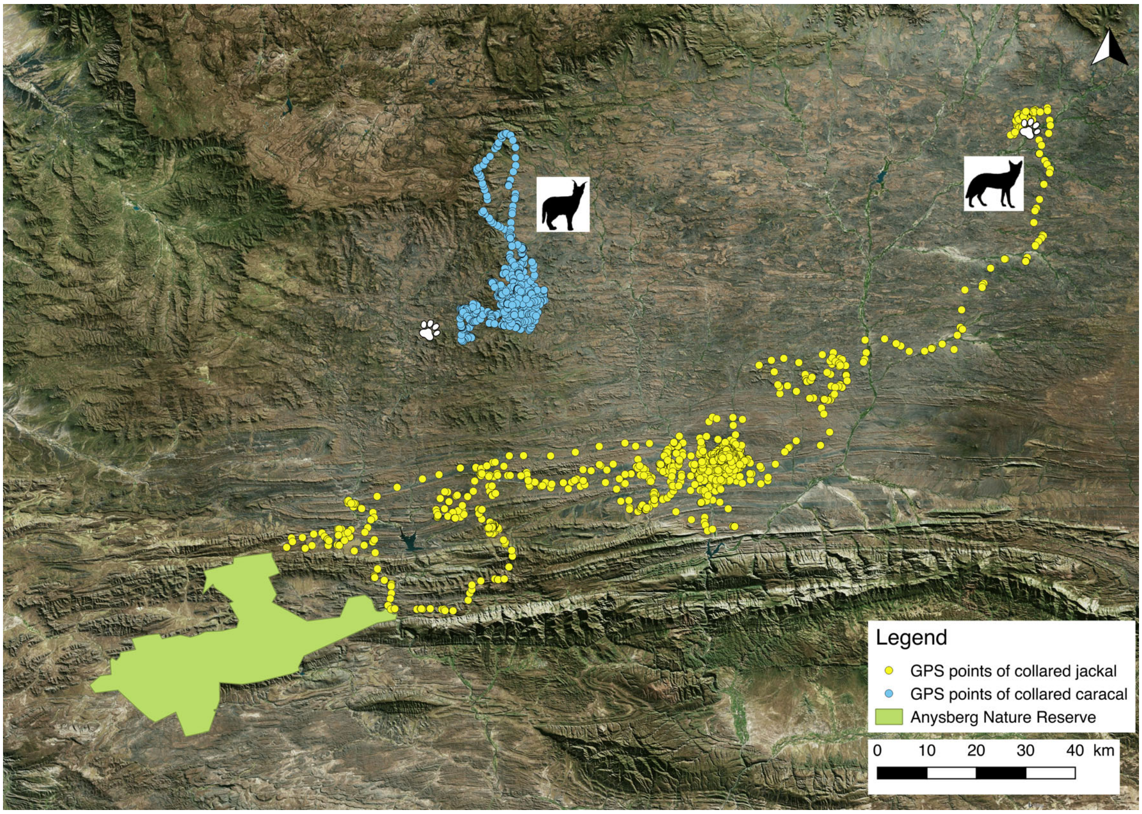

Fig. 4 GPS points of a subadult male jackal (yellow—dark grey on a grey-scale printed version) and a subadult female caracal (blue—light grey on a grey-scale printed version) dispersing across the Central Karoo despite farm fences. The jackal was monitored from the 08/05/2014 to the 17/11/2014 and the caracal was monitored from the 14/06/2014 to the 27/11/2014. The green polygon is Anysberg Nature Reserve and the paw prints represent the areas where we collared the mesopredators

significant explanatory variable for predicting livestock losses. Being closer or further away from Anysberg would have made no difference: predation was much more likely linked to whether the farm itself had accommodating attributes (notably terrain ruggedness and human presence in the form of permanent farmworkers).

CONCLUSION

The key finding of this paper is that irrespective of the precise measure of livestock losses used, and irrespective of research and measurement strategy, there was a positive correlation between the number of predators culled in the 2012/2013 season and livestock losses the following year—and this finding was robust to the inclusion of economic, demographic and geographic data. A limitation of this study is that we could not account for other (unmeasured) factors that might have caused livestock losses to change across the 2 years. However, our results are consistent with longitudinal data analysis (using the Conradie data) which could control for year (Nattrass and Conradie 2018). Another limitation is that both sources of data relied on reports by farmers. Even so, the results are consistent across data sets, and rather than providing support for the farmer narrative in favour of lethal control, the results provide support for the ecological narrative warning farmers that lethal control of predators is likely to be counter-productive in the current context.

Our findings support calls for more sustained and carefully monitored use of a variety of non-lethal measures rather than lethal control. However, jackals in particular are well known for their capacity not only to avoid traps, but also to overcome non-lethal measures such as livestock protection devices. In their recent review of the role of jackals in ecosystems, Tambling et al. (2018) warn that the jackal's 'catholic diet and a plastic behavioural repertoire' limits our ability to predict their functional response to 'landscape-level changes or manipulations'. Nattrass et al. (in press) similarly emphasise the adaptability of jackal, warning that research findings about the efficacy of both lethal and non-lethal measures will inevitably be context- and time-specific.

Treves et al. (2016) favour case-controlled experimental approaches to resolving whether lethal or non-lethal control is more effective at reducing livestock losses. Yet, the adaptability of the jackal raises questions about the extent to which findings from such studies can reliably predict the best course of action over time. Attitudes and practices amongst farmers also affect the sustainability of non-lethal approaches. A longitudinal quasi-experimental study by McManus et al. (2014) of 11 South African sheep farms found that non-lethal approaches (guard dogs or alpacas or steel collars) were more cost-effective than lethal approaches. Yet, the authors note also that less than 3 years after the end of the study, only four farmers were continuing to use only non-lethal measures, the rest had resorted to lethal control or a mixed strategy. The researchers did not comment on whether this was because the farmers considered non-lethal measures to have become less effective over time, or whether they believed that mixed and changing strategies were preferable.

According to Conradie's longitudinal survey, almost all respondents reported that in their view all forms of control, both lethal and non-lethal had become significantly less effective over time at preventing predation and that they had adapted their methods accordingly—including, worryingly, widespread illegal use of poison (Nattrass and Conradie 2018, p. 782). This suggests that socio-economically marginalised farmers faced with the recolonization of their rangelands by predators, not only resort to counter-productive lethal control, but may threaten biodiversity in other ways through indiscriminate killing techniques. Assisting these farmers, perhaps through subsidies to employ herders, or direct support from government and NGOs to develop and provide new livestock protection technologies, would make sense not only as a means of protecting their livelihoods, but to promote biodiversity and conservation in the context of rewilding and natural recolonization by predators.

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Ethical approval All procedures performed in this study involving animals and human subjects were in accordance with the ethical standards of the University of Cape Town. Ethical approval was obtained from the Commerce Faculty Ethics Committee (UCT/COM/012/2012) and the Science Faculty Animal Ethics Committee (2013V20JOR).

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