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Shepherding is not a shot in the dark: evidence of low predation losses from the Northern Cape province of South Africa

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Predation threatens the viability of livestock farming, while lethal predator management can negatively influence wildlife ecology. There is renewed interest in non-lethal vs lethal methods of livestock protection, but a systematic comparison is lacking. Using multivariate models, we explored how predator management (shepherd, no shepherd), land tenure, flock characteristics, and environmental factors drive losses of small livestock across the Northern Cape, South Africa. Black-backed jackal and caracal were the dominant livestock predators in both management groups. Predation of small livestock was five-fold lower in the shepherd (1.29% ± 0.38) compared to the non-shepherd group (6.09% ± 0.51; *p* < 0.0001), with a seven-fold lower-level of lamb predation (1.67% ± 0.51 vs. 11.52% ± 0.99; *p* < 0.0001). Predator management, livestock type, and flock size (but not land tenure or environmental factors) were predictor variables in a best-fit linear mixed effects model describing small livestock losses (*p* < 0.0001). We interpret our findings with caution because we could not control for predator and prey abundances, and the non-herder group could have inflated their predation estimates. While the efficacy of shepherding requires more research, we suggest that it is a viable predation management approach in South Africa and beyond.

Keywords: black-backed jackal, caracal, communal farmers, human–wildlife conflict, private farmers

Supplementary material: available at https://doi.org/10.2989/10220119.2022.2156610

Introduction

Carnivores have been killing domesticated livestock for centuries (Kerley et al. 2017) but recent human population growth and the expansion of agricultural activities are exacerbating livestock-carnivore, and thus human-wildlife conflict (Baker et al. 2008). Predation can threaten the viability of livestock farming directly through livestock losses, and indirectly through costs associated with mitigating predation (Yom-Tov and Ashkenazi 1995; van Niekerk 2010; Turpie and Babatopie 2018). At the same time, lethal predator management can negatively impact wildlife and their ecology (Landa et al. 1999; Yom-Tov and Ashkenazi 1995).

Predation of livestock varies widely and may be influenced by production area, the abundance of wild prey, predator management method, and cultural group (Thorn et al. 2012; Thorn et al. 2013; Odden et al. 2013). Predation estimates of small livestock in South Africa (SA) vary between 6–19% (van Niekerk 2010; Thorn et al. 2012), compared to 1.4% of total stock holdings in Namibia (Marker et al. 2003), 1.8% in Kenya (Kolowski and Holekamp 2006), 2.2% in Botswana (Schiess-Meier et al. 2007) and 4.5% in Tanzania (Holmern et al. 2007). Within a single region of SA, losses of livestock to predation (19% of total losses) were less than losses to poaching (32%) or drought (30%), but higher than fire (11%) and disease (8%) (Thorn et al. 2012). Livestock or domestic animals do not usually form the dominant part of carnivore diets despite being orders of magnitude more abundant than wild prey (Gazzola et al. 2005; Leighton et al. 2020; Middleton et al. 2021; Kamler et al. 2012). However, livestock predation can increase when wild prey abundance is limiting (Odden et al. 2013) and some predators like jackal can show a preference for domestic animals over wild (Drouilly et al. 2018).

Livestock can be protected from predation by various methods. Non-lethal livestock protection methods include fencing (predator-proof and electric), kraaling (corralling), herders/shepherds, and guardian animals, while lethal methods include call-and-shoot or capture-and-shoot (by farmers themselves or specialist hunters), foothold traps and cage traps. It should be noted that guardian dogs can hunt or scavenge both livestock and wildlife particularly when unaccompanied by a human attendant (Drouilly et al. 2020), and so their status as a non-lethal livestock protection method varies with context.

Lethal livestock protection methods in South Africa have negatively affected populations of leopard, *Panthera pardus* (Balme et al. 2010). This may have knock-on effects leading to ecosystem degradation and a loss of ecological functioning, as has been shown for other carnivores across the globe (Ripple et al. 2014; Estes et al. 2011). Many larger carnivores such as lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) have been extirpated from most of their historical range in South Africa owing, in part, to lethal predator management (van Sittert 1998; Skead 2011; Skead 2007), leaving mesopredators such as black-backed jackal (*Canis/Lupullela mesomelas*) and caracal (*Caracal caracal*) to serve as the de facto apex predators. These latter two species are currently the dominant livestock predators in South Africa (Minnie, Avenant, et al. 2018; van Niekerk 2010).

While lethal control of predators may reduce their numbers in the short term, there is no reliable scientific evidence that it provides a long-term or cost-effective solution to preventing livestock depredation (Treves et al. 2016; van Eeden et al. 2018) and can even increase it (Nattrass et al. 2020). Lethal control of predators can stimulate compensatory life history responses of predators e.g. increased populations of black-backed jackal (Minnie, Avenant, et al. 2018; Minnie, Zalewski, et al. 2018; Minnie et al. 2016) and caracal (Nattrass et al. 2020). Thus lethal methods to protect livestock from potential predators may be indiscriminate 'shots in the dark' (Treves et al. 2016). The use of non-lethal livestock protection methods are increasingly considered (Kerley et al. 2017), because these methods protect wildlife diversity, embody sustainable agricultural practices, and may be more effective in reducing livestock predation than lethal methods (Treves et al. 2016).

Several authors have suggested that herding (or shepherding when referring to small livestock such as sheep and goats) may be one of the best non-lethal interventions for reducing predation when conducted correctly (Khorozyan et al. 2017; Khorozyan and Waltert 2019; Ogada et al. 2003; Breitenmoser et al. 2005; Woodroffe et al. 2007). Shepherding is an ancient anti-predation technique used by early pastoralists (Düring 2013) and involves herding and protection of small livestock while moving between grazing areas and water points, often accompanied by kraaling of animals in a pen at night (Samuels 2013). Traditionally, nomadic herdsmen lived and moved with their livestock. In a review of non-lethal livestock management techniques across 23 countries, Khorozyan and Waltert (2019) found that only 5% of the documented 117 interventions included shepherding, highlighting a paucity in information on this practice. Shepherding is a relatively common albeit understudied practice in communal grazing areas of sub-Saharan Africa (Breitenmoser et al. 2005; du Plessis et al. 2018; Michler et al. 2019; Moritz et al. 2011; Turpie and Babatopie 2018). No published research on the use and efficacy of shepherding in South Africa exists, and this has been highlighted as a pertinent research gap by the Scientific Assessment of Livestock Predation in South Africa (du Plessis et al. 2018).

South Africa's history has resulted in different types of land tenure, broadly divided into privately held tenure predominantly encountered in commercial farming, and communally held tenure encountered mostly in subsistence farming contexts. The application of predator management methods tends to differ with land tenure and available resources (Turpie and Babatopie 2018). Most communal farmers make use of relatively low-cost methods such as herding, kraaling and other non-lethal livestock protection measures (Turpie and Babatopie 2018; du Plessis et al. 2018) that rely on cheap labour and materials (Michler et al. 2019). This is similar to other developing countries in sub-Saharan Africa (Ogada et al. 2003; Breitenmoser et al. 2005; Woodroffe et al. 2007). Nonetheless, carnivores may be killed as bycatch by communal farmers when snaring for bushmeat (Loveridge et al. 2020). In contrast, commercial livestock farmers in South Africa use both non-lethal and lethal methods to mitigate livestock predation (Turpie and Babatopie 2018; van Niekerk 2010). Traditionally, choice of these methods is based on ethics, local feasibility and personal or collective experience (Turpie and Babatopie 2018; van Eeden et al. 2018).

There is a clear need for a systematic evaluation of non-lethal and lethal livestock protection methods both globally and locally. Given the difficulty in accurately assessing the efficacy of these methods via case-control and experimental tests (Treves et al. 2016), there is a general lack of evidence-based recommendations for livestock protection in South Africa (McManus et al. 2014). This calls for alternative approaches to assess predation management techniques aimed at: (1) providing baseline information on the efficacy of management techniques, and (2) identifying testable hypotheses/predictions to direct future research using appropriate experimental designs. Here, we used an unplanned experimental design where we combined two distinct, but comparable data sets collected via different methods to test whether shepherding reduces predation of small livestock (sheep *Ovis aries* and goats *Capra hircus*), regardless of land tenure. Specifically, we assessed the impact of shepherding vs. non-shepherding practices on small livestock predation in the arid Northern Cape province of South Africa, which, at 13%, has one of the highest-reported livestock predation levels in the country (Turpie and Babatopie 2018). We hypothesised that shepherding would be more effective in reducing predation on small livestock relative to other methods for the dominant predators of small livestock. This represents a first exploratory step in testing the efficacy of shepherding as a viable predation management approach in South Africa.

Materials and methods

Study site

Farms in the study were all located in the Namaqua District of the Northern Cape province of South Africa, which includes the dry Succulent and Nama Karoo biomes (Mucina and Rutherford 2006) and is an important extensive animal production area (de Waal 1990). Data came from two distinct data sets (see *Data sources*) but are comparable in having similar farming land use with small livestock (sheep and goats), predators, climate (arid desert, Köppen-Geiger classification; Beck et al. 2018), lithology (leptosol and/or rhodosol soils; van Engelen and Dijkshoorn 2013), landforms (plains and/or medium grade mountains; van Engelen and Dijkshoorn 2013), and somewhat similar surface roughness (low to intermediate; Figure 1) but different net primary productivity. Surface roughness (hereafter roughness) is the variation in elevation and is recognised as an important measure of habitat complexity that determines behaviour of both wild and domesticated animals (Sappington et al. 2007). Roughness was calculated in QGIS v. 3.22.3 based on the locations of farms on a 30-m digital elevation model (Farr et al. 2007). Net primary productivity (NPP) has been variably correlated with predation of livestock and herbivores (Letnic et al. 2017; Graham et al. 2005). We measured NPP at farm locations over the period encompassing the two data sets (2007–2016) via the global MODIS Terra data product at 500 m resolution (Running and Zhao 2019). No relevant mammalian population density data could be found on global databases, e.g. TetraDENSITY (Santini et al. 2018).

Data sources

Data were collected via two methods (observations of kills vs. interviews), on two different land tenure types (communal vs. private small livestock farms), and at different temporal scales (daily vs. yearly) as described in detail in Table S1. Social-ecological studies such as those on human-wildlife conflict span ecological, spatial, and socio-economic variables. In response to their challenging and interdisciplinary nature, several social-ecological studies have successfully integrated data from different sources (Carter et al. 2020; Behr et al. 2017). Integration of distinct data sets, collected using different methods, may even provide more or better information than single data sets (Zipkin et al. 2019). This is also part of an increasing trend to assess ecological processes operating at large spatial scales (Zipkin et al. 2021). Critically for our study, data sets differ in the presence or absence of shepherds, and in the type of predator management (non-lethal or lethal). Our data sets lack predator and natural prey densities, but we confirmed that the same predators were responsible for predation in the two groups. Large felids can kill more large stock when their wild prey reaches a minimum threshold but this relationship is not clear for small stock (Khorozyan et al. 2015). We acknowledge that these are distinct data sources, but data sets for the direct comparison between communal and private farmers, and between groups with and without shepherds are not available. Thus, these data sets provided an important opportunity to test the hypothesis on shepherding efficacy.

The shepherd data set (field observations)

The shepherding group was in the western Namaqua District within the Succulent Karoo biome (Figure 1). Data comprised hourly, and daily field observations made by shepherds on 11 farms (six communally- and five privately-owned) between 2012 and 2016 (Table S1). Predation events were recorded on mobile devices by shepherds trained to recognise tracks and signs of wildlife and predation marks on carcasses. Where possible, signs of predation were photographed, and verified by researchers. The shepherd group comprised communal and private farms that were available as part of the South African government's Expanded Public Works Programme (EPWP) implemented by South African National Parks (SANParks). This group of livestock owners with herders were all in the Kamiesberg area and had signed agreements to use herders as part of a sustainable farming initiative with Conservation International (CI). This non-random sample could bias the outcome, for example if the farmers were motivated to record less livestock losses as part of the study. However, this bias is unlikely since it was herders who were independently paid to keep accurate records, with no incentive to bias records.

Shepherds stayed with the flock while they grazed during the day and camped at stock posts with the flock at night, using various non-lethal management methods such as bell collars on small livestock, livestock guardian dogs and kraals (Table S1). All guardian dogs were accompanied by human attendants (and fed daily) in this study, thus mitigating scavenging and hunting of either livestock or wildlife (Drouilly et al. 2020). Losses of small livestock were calculated per month, and subsequently summed per annum and expressed as a proportion of the average flock size in that year to allow comparison with the non-shepherd data sets, which was collected on an annual basis.

The non-shepherd data set (interviews)

The non-shepherd data set was a sub-set of a national survey of private livestock farmers in 2006 and 2007 by van Niekerk (2010). Data used included farms in the Succulent and Nama Karoo part of the Namaqua District (Figure 1). The number of farmers interviewed was based on the percentage that each of the different magisterial districts per province contributed to the total small livestock populations (sheep and goat) of South Africa. Thereafter, potential interviewees were randomly selected from a list provided by livestock producer organisations. From this data set, we selected only those farms within the Namaqua District (n = 103) to allow comparison with the shepherding group. Farmers were interviewed telephonically following a structured questionnaire to provide an estimate of livestock types, age classes, flock size, as well as losses of small livestock in each category (van Niekerk 2010). This group used a mixture of non-lethal (largely electric and jackal-proof fencing but not herding) and lethal approaches (largely foothold traps, or cage traps combined with shooting). Some (11%) of these farmers did not use lethal predator management (Table S1).

Statistical analyses

All statistics were performed in R software v. 4.2.0 (RCoreTeam 2020). Percentage data from losses of small livestock were bounded and zero-inflated and thus logit-transformed so that the distribution of residuals met assumptions of analyses used. Predation percentages of sheep, lambs, goats, and kids were compared between shepherding and non-shepherding groups using ANOVAs followed by post-hoc Tukey tests. The relative contribution

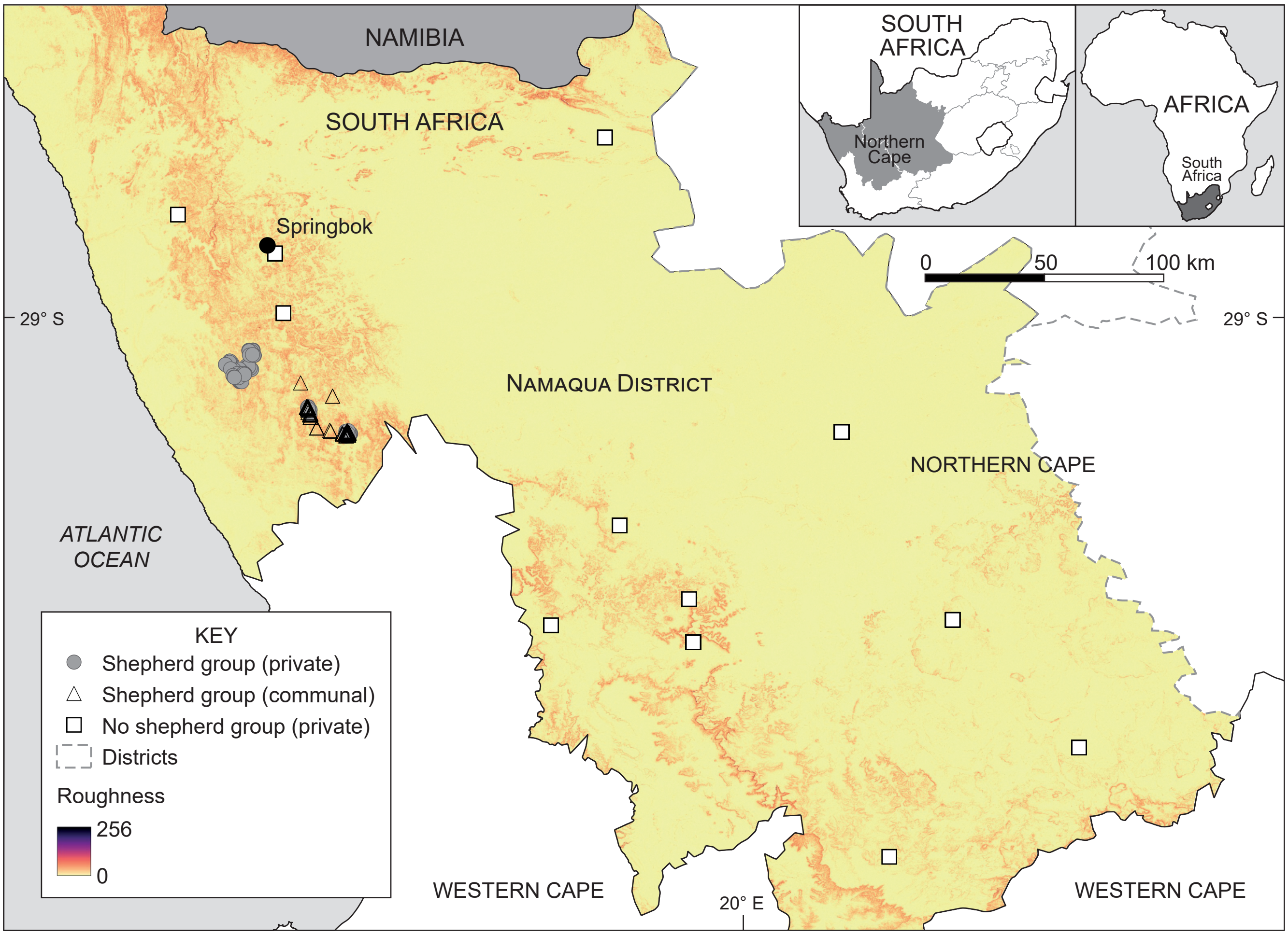

Figure 1: Location of farms in the study within the Namaqua District, Northern Cape, South Africa. The inset maps show Africa and South Africa, with the shading indicating the study area. The base map indicates surface roughness of the terrain (unitless index 0–256). Some points are in proximity and overlap

to predation ascribed to each predator species was calculated as the sum of mortalities per predator species relative to total predation, for both groups.

Eight variables thought to influence predation (Table 1) were assessed for their importance using a boosted regression tree (BRT) model following Elith et al. (2008) via the 'dismo' package in R (gaussian family, step size of 20, tree complexity of 10, slow learning rate of 0.001, and bag fraction of 0.7). The relative influence of each explanatory variable reported by the BRT model determined their order in linear mixed effects models (LME), using the 'lme4' package (Bates et al. 2015). In LMEs, predator management (i.e. shepherd vs. non-shepherd groups), land tenure, livestock type, NPP, predator type and roughness were considered fixed effects while repeated measures of farm identity and flock size were considered random effects (Table 1). By default, random effects are the final term in 'lme4' models, irrespective of their influence.

We used Akaike Information Criterion (AIC) model selection to distinguish among a set of possible LME models to find the best-fit model describing drivers of livestock loss. The most parsimonious model was one that had the lowest AIC value, a ΔAIC between the null (N) and test (T) models of at least 2, and $p \leq 0.05$). The N model always excluded the main fixed effect of interest (predator management method) while the T model contained it. The significance of LME models was assessed using the maximum likelihood test, which produces a p and χ^2 value for each pair of N and T models. The significance of fixed terms within the model were assessed using t-tests via Satterthwaite's method ('lmerModLmerTest' function), while random effects were assessed via ANOVA-like tables ('ranova' function). We note that LMEs were considered more suitable than repeated measures or multi-factor ANOVAs (Pinheiro and Bates 2000) since they do not assume independence of predictor variables (flock sizes varied with land tenure and management, i.e. were not independent) and can account for bounded (proportional) data (predation as a percentage of flock size), clustering (management types within land tenures and locations), and unbalanced designs (different number of repeated measures between groups). All models presented met assumptions of linearity, homoscedasticity, and normality.

Human and animal ethics

All human participants were adults and informed about the study, of their rights to anonymity and freedom to join or leave the study, after which they signed a consent form. All animals were managed by their owners as part of routine farm operations.

Results

Comparison of data sets

Farmers in both data sets managed small livestock. Most (99.7%) of the flock were sheep in the non-shepherd or interviewed group, while the shepherd or observation group managed both sheep (ca. 58.8% of herd) and goats (41.2% of the flock, Table S1). The relative contribution that each predator species made to predation was similar in the non-shepherd and the shepherd data sets (p = 0.758, df = 1, F = 0.095) where black-backed jackal and caracal were identified as the dominant predators in both data sets (Figure 2). Black-backed jackal contributed to 62% and 46% of predation while caracal contributed about 37% and 45% of predation for non-shepherd and shepherd data sets respectively (Figure 2). Irrespective of the data set, black-backed jackals killed marginally more livestock than caracal (p = 0.055). Shepherds reported that baboons (*Papio ursinus*, n = 5 instances, 13.5% of predation) and leopards (n = 1 instance, 2.7% of predation) also killed livestock. Interviewed farmers in the non-shepherd group did not mention baboons and leopards as predators of sheep and goats but ascribed some predation to feral dogs (*Canis familiaris*, n = 3 instances, 1.4% of predation; Figure 2). Along with the similarity in biome, topography and land use, the similarity between interview and observation data sets regarding the dominant predators and the contribution that they made to predation of small livestock supports our assumption that the data sets can be compared to test our hypothesis.

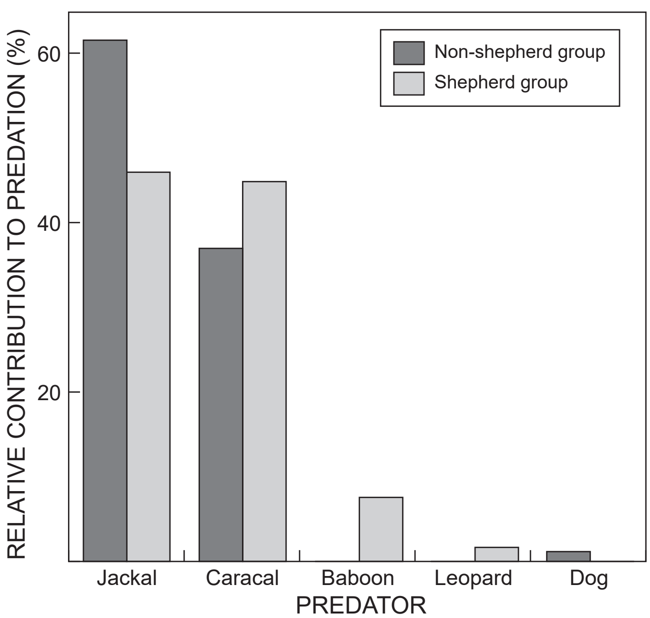

Figure 2: Relative contribution to predation ascribed to each predator according to interviews (non-shepherd group) or observations (shepherd group) in the Northern Cape province, South Africa

Livestock losses from various causes

The shepherd group reported several sources of small livestock losses including diseases, exposure, predation, theft, and other (unknown) causes, while the non-shepherd group only reported on predation, theft, and other causes. Thus, only the latter three reasons for losses were comparable between management groups (Figure S1a). Here, livestock loss differed between management methods (p < 0.0001, df = 1, F = 21.3) and different causes of loss (p < 0.0001, df = 2, F = 17.5) with no interaction. Predation was lower when a shepherd was present compared to no shepherd (p < 0.0001), while there was no difference in small livestock losses from theft or 'other' causes between these management groups (Figure S1a). Diseases and exposure caused comparable mortality to predation based on the non-shepherd group (p > 0.05; Figure S1b) but up to about 20% of the flock could be lost from disease or exposure (Figure S1b). Shepherds reported no losses from theft, but this was not different to other causes of loss due to high variation in the data (Figure S1b). Other causes of small livestock losses (vehicle collisions, fights between stock, and being caught in traps set for predators) accounted for less than 1% each and were reported in only a few instances (n = 1 for fight, n = 2 for vehicle and trap) in the shepherd group. Overall and regardless of the cause of loss, farmers using shepherding reported lower losses (2.32% ± 0.46) of small livestock compared to farmers who did not use shepherding (5.15% ± 0.44; p > 0.0001, df = 1, F = 27.9).

Small livestock losses from predation

According to the BRT model (R^2 = 0.46), the specific farm was the most important predictor of livestock losses from predation (35%), closely followed by the type of management to protect livestock, i.e. the presence of a herder or not (32%). Flock size (23%) and the type of predator responsible for livestock losses (9%) were also important predictors. Surface roughness had a small influence of 0.5%. Although the 10-year average NPP was higher in the herder vs. the non-herder group (0.32 ± 0.009 vs. 0.14 ± 0.007 kg C m^2 yr^{-1}, p < 0.0001, one-way ANOVA), the influence on livestock losses was negligible at 0.2%. Land tenure and livestock type had the smallest influences at 0.02% and 0.01%, respectively.

The negligible influence of land tenure on predation is important because, together with the similarity in predators involved, it indicates that farmers experienced similar predation issues and drivers of predation, irrespective of land tenure. Supporting this, subsequent LMEs identified land tenure as an exact linear combination of other covariates (r > 0.7) and land tenure was excluded from LMEs. The BRT was useful in determining the order in which potential explanatory variables could be used in subsequent LME models. Despite their low influence in the BRT model, NPP, roughness and livestock type were included in the LME as parameters of interest. Data input for the LMEs was at an annual time scale to allow standardisation between interview and observation data sets. For this reason, predator type could not be used in the models because several predators were responsible for livestock loss at any one annual time point. Thus, all variables except predation and land tenure (Table 1) were used as inputs for LMEs in the order: management, surface roughness, NPP, livestock type (fixed variables) with farm identity and flock size as random variables (placed after fixed variables as per the default in LMEs; Table 2).

Total livestock predation was lower ($p < 0.0001$, df = 1, $F = 27.1$) with shepherding (1.29% ± 0.38) compared to without shepherding (6.09% ± 0.51; Figure 3). Predation also depended on the livestock type with more lambs being killed compared to other types and age classes ($p < 0.0001$, df = 4, $F = 203.0$; Figure 3). The best-fit LME model describing small livestock predation comprised the parameters: predator management (shepherd vs. non-shepherd), livestock type, farm identity and flock size (model T3, $p = 0.0001$, ΔAIC = 13; Table 2). This model carried 63% of the predictive power (or AIC weight) of the full set of models being considered (Table 2). Management, presence of sheep and lambs, and flock size (but not farm identity) were the most important variables in the T3 model (Table 3).

Table 1: Predictor variables used in the boosted regression trees to determine their use and order in linear mixed effects models

Variable	Description	Type	Effect type
Farm	Anonymised farm number	Numerical	Random
Flock size	Average annual flock size	Numerical	Random
Land tenure	Communal- and private farms	Categorical	Fixed
Livestock type	Sheep, lambs, goats, and kids	Categorical	Fixed
Management	Shepherd- and non-shepherd	Categorical	Fixed
NPP	Net Primary Productivity (2007–2016)	Numerical	Fixed
Predator type	Predator species	Categorical	Fixed
Roughness	Variation in elevation over the terrain	Numerical	Fixed

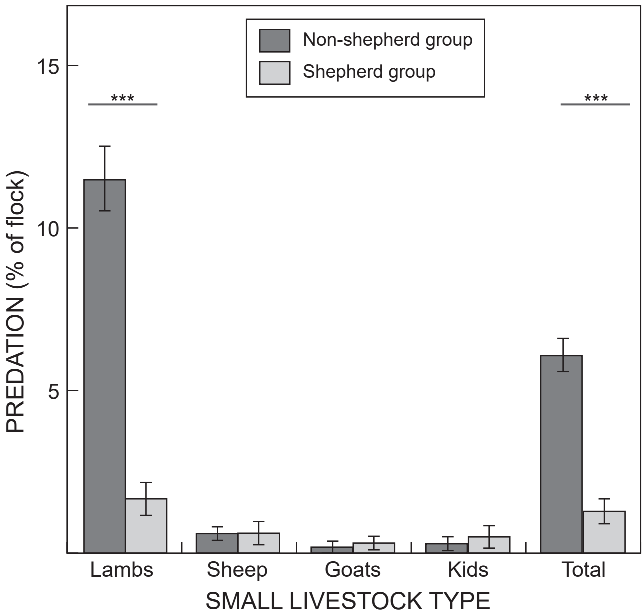

Figure 3: Comparison of predation of small livestock (mean percentage of herd ± SE) per livestock type and age class between farms with or without shepherding in the Northern Cape Province, South Africa. Significant differences at the $p < 0.0001$ level are indicated by ***

Table 2: The Null (N) and Test (T) linear mixed effects models explaining the variation in predation on (a) all small livestock and (b) lambs in Northern Cape farms, South Africa. Test models (T) are always compared to the corresponding null model (N) without the main response variable of interest, i.e., predator management. The most parsimonious model is in bold (model with the lowest Akaike information criterion (AIC) value, a ΔAIC between N and T models of at least 2, and $p \leq 0.05$). Alternative combinations of parameters did not change the outcome

	df	AIC	ΔAIC	AIC weight	Log Likelihood	X^2	*p*-value
(a) Small livestock predation models							
N1 = Losses ~ Roughness + NPP + Type + (1|Farm) + (1|Flock size)		2253		0.01	–1117		
T1 = Losses ~ Management + Roughness + NPP + Type + (1|Farm) + (1|Flock size)	1	2248	5	0.10	–1114	6.6	0.0099
N2 = Losses ~ NPP + Type + (1|Farm) + (1|Flock size)		2292		0.02	–1122		
T2 = Losses ~ Management + NPP + Type + (1|Farm) + (1|Flock size)	1	2292	0	0.24	–1118	7.3	0.0069
N3 = Losses ~ Type + (1|Farm) + (1|Flock size)		2257		0.00	–1122		
T3 = Losses ~ Management + Type + (1|Farm) + (1|Flock size)	**1**	**2244**	**13**	**0.63**	**–1114**	**14.8**	**0.0001**
N4 = Losses ~ (1|Farm) + (1|Flock size)		2379		0.00	–1186		
T4 = Losses ~ Management + (1|Farm) + (1|Flock size)	1	2361	18	0.00	–1176	20.4	<0.0001
N5 = Losses ~ (1|Flock size)		2378		0.00	–1186		
T5 = Losses ~ Management + (1|Flock size)	1	2359	19	0.00	–1176	20.9	<0.0001
(b) Lamb predation models							
N6 = Losses ~ Roughness + NPP + (1|Farm) + (1|Flock size)		294		0.01	–141	8.7	0.0032
T6 = Losses ~ Management + Roughness + NPP + (1|Farm) + (1|Flock size)	1	287	7	0.19	–136		
N7 = Losses ~ NPP + (1|Farm) + (1|Flock size)		294		0.01	–142	16.1	<0.0001
T7 = Losses ~ Management + NPP + (1|Farm) + (1|Flock size)	1	286	8	0.29	–137	9.8	0.0017
N8 = Losses ~ (1|Farm) + (1|Flock size)		302		0.00	–147		
T8 = Losses ~ Management + (1|Farm) + (1|Flock size)	**1**	**285**	**17**	**0.50**	**–138**	**18.9**	**<0.0001**

Similar to total livestock losses, lamb predation was lower ($p < 0.0001$, df = 1, $F = 25.21$) with shepherding (1.67% ± 0.51) compared to without shepherding (11.52% ± 0.99; Figure 3). The best-fit LME model for lamb predation included predator management, the flock size of lambs and farm identity (T8, $p < 0.0001$, ΔAIC = 17; Table 2). This model carried 50% of the predictive power (or AIC weight) of the full set of models being considered (Table 2). While contributing to the best-fit model, flock size ($p = 0.827$) and farm identity ($p = 1.00$) were poor predictors of lamb predation (Table 3), thus predator management was the only important predictor in the model for lamb predation ($p < 0.0001$; Table 3). Predation of small livestock was driven by lamb predation since predation of sheep, goats and kids was very low in both management groups (< 1%) and did not differ between groups (Figure 3). Consequently, no best combination of predictor variables for sheep, goat and kid predation could be identified in the LMEs.

Flock size emerged as a predictor of total livestock losses in LMEs but the relationship appeared to be neutral to weakly negative, possibly depending on thresholds of flock size (Figure 4). There appeared to be no relationship between predation and flock size at relatively small flock sizes (20 to 2 000 in the shepherd group) but a slight negative relationship appeared at larger flock sizes up to 21 000 (Figure 4). We interpret these results about relatively larger flock sizes with caution because only a few (10) farms with 3 000 or more small livestock determined the relationship (Figure 4).

Discussion

Validity of our approach

Three major approaches can be used to study livestock predation (direct monitoring of livestock, face-to-face interviews, and telephonic interviews of livestock managers), all with varying accuracy and biases (Knowlton et al. 1999). The resulting estimates of losses due to predation will likely differ, but conclusions based on distinct data sets can be moderated if the methodology is explicitly described. The present study utilised two distinct data sets that reveal two important findings regarding the efficacy of shepherding and the scale of livestock predation relative to other forms of livestock loss.

We highlight an important opportunity to use distinct, but complimentary, data sets in addressing under-researched and data-scarce research areas where relevant data may not be available. Reviews of various predation management techniques and their efficacy in reducing livestock predation (Eklund et al. 2017; van Eeden et al. 2018) emphasise that few studies used a case-control study design, considered the 'gold standard', thus hampering evidence-based

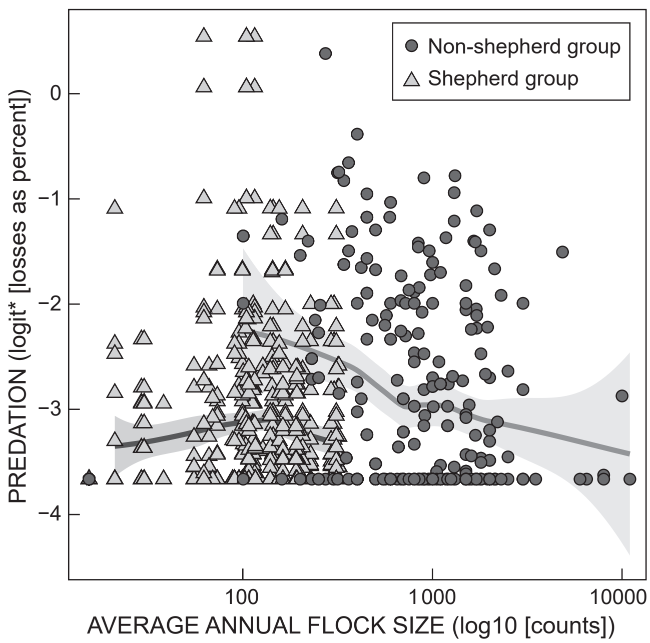

Figure 4: The relationship between flock size and predation of small livestock on farms with or without shepherding in the Northern Cape province, South Africa

Table 3: Coefficients and importance (p-values) of each predictor variable in the most parsimonious linear mixed effects models (Table 2) describing predation of (a) all small livestock and (b) lambs in Northern Cape farms, South Africa. Satterwaite's post-model variance test and an ANOVA-like table were used to test the importance of fixed effects and random effects, respectively. The most important model parameters are indicated by bolded p-values

(a) Small livestock predation model (T3)					
Fixed effects	Estimate	Standard error	df	*t*-value	*p*-value
Management	–0.272	0.0698	194	–3.89	**0.0001**
Kids	0.053	0.0654	899	0.81	0.4186
Lambs	0.425	0.0942	162	4.51	**<0.0001**
Sheep	–0.384	0.0955	151	–4.02	**<0.0001**
Random effects	Log likelihood	Likelihood ratio test			
Farm identity	–1114	0	1	n/a	1.00
Flock size	–1189	150	1	n/a	**<0.0001**
(b) Lamb predation model (T8)					
Fixed effects	Estimate	Standard error	df	*t*-value	*p*-value
Management	–1.14	0.234	109	–4.87	**<0.0001**
Random effect	Log likelihood	Likelihood ratio test			
Farm identity	–138	0.000	1	n/a	1.00
Lamb flock size	38	0.047	1	n/a	0.8277

management of carnivore-livestock conflict. Currently, the application of most livestock and predation management methods are based on ethics, local feasibility and personal or collective experiences (van Eeden et al. 2018; Thorn et al. 2012), largely due to the difficulty in accurately assessing the efficacy of these methods (Treves et al. 2016). As such, many predation management methods remain untested and represent 'shots in the dark' (Treves et al. 2016).

Given the general lack of information relating to the efficacy of various livestock and predation management strategies in South Africa (du Plessis et al. 2018) and elsewhere (van Eeden et al. 2018), the consolidation of different data sets provides a valuable and under-utilised opportunity to conduct analyses into the efficacy of these management strategies. This approach is increasingly used to address novel, socio-ecological hypotheses about carnivore-livestock and human-wildlife conflict (Zipkin et al. 2019; Nattrass and Conradie 2013). Although this approach may be prone to errors (Eklund et al. 2017), it fills an important gap in our understanding by (1) recognising general trends in data, and (2) identifying hypotheses aimed at directing future research via case-control study designs. In our study, we could justify the combination of two distinct data sets, to successfully address hypotheses where data are lacking.

We justified the consolidation of distinct data sets by testing their similarity independent of the subject of interest, i.e. shepherding efficacy. Black-backed jackal and caracal were identified as the dominant causes of livestock predation, as is the case on livestock farms across South Africa (Drouilly et al. 2018; Humphries et al. 2016; Minnie, Avenant, et al. 2018; van Niekerk 2010). Unfortunately, data on the abundances and densities of these predators and their wild prey were not available for our data sets and we cannot rule out the influence of wild prey densities on livestock losses. Collecting wildlife scat and GPS positioning data to approximate animal density was beyond the financial scope of this present study, which relied on existing data. Relatively low densities of natural prey animals can drive increased predation of livestock (Khorozyan et al. 2015; Odden et al. 2013), but this has not been shown for small stock in South Africa and further abroad (Khorozyan et al. 2015). We think it is possible that the predator and wild prey densities were similar in the two data sets because of similarities in climate, geology, habitat types, land use, and predators involved. While NPP, another potential driver of predation (Graham et al. 2005), was higher in communal areas, it was not important in describing livestock losses as evidence from our best-fit models. Finally, we cannot exclude the possibility of inflated predation estimates in the interview data set, as farmers may assign livestock losses to predators in the absence of direct evidence (Nattrass et al. 2020).

Efficacy of shepherding against predation

In our study, farms with shepherds had five-fold lower levels of livestock losses to predators than farms without shepherds, irrespective of land tenure or environmental variables (NPP, roughness). Another predictor of small livestock predation was herd size but the direction of this relationship was unclear. Our results must be interpreted with caution because, as mentioned, we were not able to control for important variables that are known to influence livestock depredation (including predator and prey abundances) or reporting bias. Despite the limitations of this study, our findings are consistent with the global reviews indicating the relative efficacy of non-lethal vs. lethal predator management (van Eeden et al. 2018; Treves et al. 2016; Eklund et al. 2017; Miller et al. 2016).

Given the predominance of sheep farming in the study area and the tendency of small- to medium-sized predators to prey on small or young animals (Sangay and Vernes 2008; Somers et al. 2018), it is assumed that black-backed jackal and caracal prey on lambs and this was supported by our results. Thus, the seven-fold lower level of in lamb predation with shepherding vs. without shepherding was a particularly important finding for extensive arid rangelands where small livestock predominate.

Further, the fact that land tenure did not drive livestock predation according to LMEs, suggests that shepherding may be equally useful to communal farmers with small herds and private farmers with larger herds. Nevertheless, barriers to the use of shepherding and kraaling of large herds owned by private, commercial producers may exist and need novel solutions. Other studies, using case-control study designs, have documented that shepherding reduces livestock predation by wolves (*Canis lupus*) (Iliopoulos et al. 2017), coyote (*Canis latrans*), puma (*Puma concolor*), black bears *(Ursus americanus*) (Palmer et al. 2010), lions, leopards and spotted hyenas (Woodroffe et al. 2007). For example, using shepherds resulted in a two- to four-fold reduction in livestock losses ascribed to wolves in Greece (Iliopoulos et al. 2017). Bruns et al. (2020) recently showed that shepherding resulted in a 97% reduction in livestock predation by wolves, although this was based on a single sample. Similarly, Woodroffe et al. (2007) reported a reduced probability of large carnivore predation with an increase in the number of shepherds. Accordingly, several authors have suggested that shepherding could be one of the best interventions for reducing predation when applied correctly (Khorozyan et al. 2017; Khorozyan and Waltert 2019; Breitenmoser et al. 2005; Ogada et al. 2003; Woodroffe et al. 2007), where human presence and animal husbandry was linked to this efficacy (Ogada et al. 2003; Woodroffe et al. 2007).

Conversely, some studies have reported that shepherds do not necessarily reduce livestock predation. This may be ascribed to the inability of timid shepherds to deter large predators such as leopards (Khorozyan et al. 2017), inattentive shepherds focused on other tasks such as fence maintenance (Palmer et al. 2010) or socialising with each other, e.g. child shepherds (Woodroffe et al. 2007), or inadequate training of shepherds and guardian dogs (Khorozyan et al. 2017). These conflicting results from various studies highlights that there is no such thing as a silver bullet, and more research in various contexts and scales is needed. Nonetheless, our results are a valuable first step that should motivate further testing of shepherding efficacy in the process of developing evidence-based management.

Placing predation in context

Predation placed in perspective with other causes of livestock mortality and loss is useful to gauge its relative impact. Globally, drought and disease account for the main losses of livestock (30% for drought and 9–52% for disease; FAO (2018)) but are seldom compared with the relatively lower losses (5%) reported for predation (Baker et al. 2008). In our study, average predation of small livestock was relatively low in absolute terms (1–6%) irrespective of management. This is lower than the values of 6–19% previously reported for South Africa (van Niekerk 2010; Turpie and Babatopie 2018; Thorn et al. 2012; Nattrass et al. 2020; Drouilly et al. 2018; Kamler et al. 2012; Humphries et al. 2016) but consistent with the 2–8% for southern Africa (Verschueren et al. 2020; Kolowski and Holekamp 2006; Schiess-Meier et al. 2007; Franco et al. 2018). These estimates align well with global estimates of predation of livestock, which are lower than other sources of mortality. Based on our information from the shepherd group, livestock losses from disease and exposure were as important as predation. It is likely that direct observations were more accurate in confirming the cause of mortality than questionnaire surveys, as the shepherds involved were trained to recognise tracks and signs of predators including bite marks on livestock, while also being present to distinguish predation from other causes of death such as disease and exposure. Together with global assessments, this implies that losses from disease and exposure may be generally as high or higher than losses from predation in South Africa, a hypothesis that could be tested by controlled studies across a wider area.

Research needs

Several research questions arise out of this and similar work. Given the high variability in the efficacy of most livestock and predation management techniques in reducing livestock predation (Miller et al. 2016), the applicability, efficacy and cost-effectiveness of any management technique appears to be context dependent. Ideally, several studies across multiple contexts (livestock types, breeds and ages, socio-economic and cultural status of the farming community, environmental conditions, grazing pattern, dominant predator, geographic region, etc.) are required to ascertain the usefulness of shepherding in reducing livestock predation (Miller et al. 2016). For example, the Before-After-Control-Impact (BACI) approach, considered a 'gold standard' (Treves et al. 2016) could consider predation alongside other causes of stock loss and mortality and would compare them under different predator management approaches across multiple environments. Such a challenging analysis would need careful collaboration between producers, wildlife managers and scientists (Knowlton et al. 1999) while a consortium approach could be encouraged by funders. Besides predation, we found that average mortality of livestock from all measured causes was lower (about 2%) for farmers employing shepherds compared to those not using shepherds (about 5%). While we again interpret this with caution due to imbalances in reporting on causes of loss, it provides another testable hypothesis, namely that shepherds can reduce not only predation but also livestock mortality due to other causes, e.g. by providing timeous responses to ill, injured, or lost animals. Additional management benefits of shepherds that could be tested include general animal husbandry, detecting damage to infrastructure (fences, water points), assessing grazing conditions (du Plessis et al. 2018) and promoting the recovery of biodiversity in agroecosystems (Schurch et al. 2021).

Finally, innovative research could take the form of appropriately harmonising data sets from different sources, e.g. research based on both observations of kills and interviews/questionnaires concurrently so that biases emerging from either data collection method could be ameliorated, while providing indications of social perceptions. Possible biases could be present in our data and would benefit from such a study. Observations of kills may underestimate livestock predation in cases where livestock herds are dispersed over large grazing areas and the shepherd can only tend to a portion of the flock, thus missing potential kills. Similarly, observations of carnivores scavenging on carcasses may overestimate livestock predation by incorrectly assigning livestock mortality to the scavenger (Somers et al. 2018). In addition, the efficacy of shepherds in detecting livestock carcasses may be influenced by the work ethic of the individual shepherds or habitat. In contrast, data collected from questionnaires and interviews may overestimate livestock predation (Nattrass et al. 2020), especially when respondents base these values on total livestock counts instead of actual observation of carcasses and the identification of the responsible predators. Research that ground-truthed presence-absence data for the Asiatic black bear, *Ursus thibetanus* (Liu et al. 2009), obtained from questionnaires indicated no difference between questionnaire and ground-truthed data. However, such data is non-existent for livestock predation and thus represents a valuable future research opportunity.

Policy implications

Until controlled, comparative studies of lethal and non-lethal predator management have been published, we can only generalise available findings from this and other studies while applying the precautionary principle. Our results suggest that non-lethal predator management methods are effective locally and this supports strong evidence from abroad (Treves et al. 2016; Treves and Naughton-Treves 2005). According to Knowlton et al. (1999), preferred solutions to predation should be as non-intrusive and benign as possible. We thus recommend that legislation on damage-causing animals foster the coexistence of livestock and wildlife and limit or suspend lethal approaches to predator control.

Conclusion

We find that shepherding is not a shot in the dark, as small livestock predation was lower with shepherds present. While the use of shepherding requires more research and may have several barriers to its use, it is a potentially low-cost, non-harm approach to predator management while also providing livelihoods. Reviving practical forms of shepherding in a range of land tenure and socio-economic contexts, both in the developing and developed world, could support traditional cultural practices, and has the potential to elevate the practice to be a vital part of animal husbandry and farm management.

Data availability — This review adheres to FAIR data. Associated data and code are available at https://doi.org/10.5281/zenodo.7351472. Further information and requests for resources should be directed to and will be fulfilled by the lead contact, HJ Hawkins.

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References

Baker PJ, Boitan L, Harris S, Saunders G, White PCL. 2008. Terrestrial carnivores and human food production: impact and management. *Mammal Reviews* 38: 123–166. https://doi.org/10.1111/j.1365-2907.2008.00122.x.

Balme GA, Slotow R, Hunter LTB. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation* 13: 315–323. https://doi.org/10.1111/j.1469-1795.2009.00342.x.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–51. https://doi.org/10.18637/jss.v067.i01.

Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF. 2018. Present and future Koppen-Geiger climate classification maps at 1-km resolution. *Scientific Data* 5: 180214. https://doi.org/10.1038/sdata.2018.214.

Behr DM, Ozgul A, Cozzi G, Durant S. 2017. Combining human acceptance and habitat suitability in a unified socio-ecological suitability model: a case study of the wolf in Switzerland. *Journal of Applied Ecology* 54: 1919–1929. https://doi.org/10.1111/1365-2664.12880.

Breitenmoser U, Angst C, Landry J-M, Breitenmoser-Würsten C, Linnell JDC, Weber J-M, Woodroffe R, Thirgood S, Rabinowitz A. 2005. Non-lethal techniques for reducing depredation. In: Woodroffe R, Thirgood S, Rabinowitz A (eds.), *People and Wildlife*. Cambridge: Cambridge University Press. pp 49–71.

Bruns A, Waltert M, Khorozyan I. 2020. The effectiveness of livestock protection measures against wolves (*Canis lupus*) and implications for their co-existence with humans. *Global Ecology and Conservation* 21: e00868. https://doi.org/10.1016/j.gecco.2019.e00868.

Carter N, Williamson MA, Gilbert S, Lischka SA, Prugh LR, Lawler JJ, Metcalf AL, Jacob AL, Beltrán BJ, Castro AJ, et al. 2020. Integrated spatial analysis for human-wildlife coexistence in the American West. *Environmental Research Letters* 15: 1–7. https://doi.org/10.1088/1748-9326/ab60e1.

de Waal HO. 1990. Animal production from native pasture (veld) in the Free State Region – A perspective of the grazing ruminant. *South African Journal of Animal Science* 20: 1–9. https://doi.org/10.4314/SAJAS.V20I1.

Drouilly M, Kelly C, Cristescu B, Teichman KJ, O'Riain MJ. 2020. Investigating the hidden costs of livestock guarding dogs: a case study in Namaqualand, South Africa. *Journal of Vertebrate Biology* 69. https://doi.org/10.25225/jvb.20033.

Drouilly M, Nattrass N, O'Riain MJ. 2018. Dietary niche relationships among predators on farmland and a protected area. *The Journal of Wildlife Management* 82: 507–518. https://doi.org/10.1002/jwmg.21407.

du Plessis JJ, Avenant NL, Botha A, Mkhize NR, Müller L, Mzileni N, O'Riain MJ, Parker DM, Potgieter G, Richardson PRK, et al. 2018. Past and current management of predation on livestock. In: Kerley GIH, Wilson SL, Balfour D (eds.), *Livestock Predation and its Management in South Africa: a Scientific Assessment*. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela University. pp 125–177.

Düring BS. 2013. Breaking the bond: Investigating the Neolithic expansion in Asia Minor in the seventh millennium BC. *Journal of World Prehistory* 26: 75–100. https://doi.org/10.1007/s10963-013-9065-6.

Eklund A, Lopez-Bao JV, Tourani M, Chapron G, Frank J. 2017. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific Reports* 7: 1–9. https://doi.org/10.1038/s41598-017-02323-w.

Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, et al. 2011. Trophic downgrading of planet Earth. *Science* 333: 301–306. https://doi.org/10.1126/science.1205106.

FAO. 2018. *The Impact of Disasters and Crises on Agriculture and Food Security: 2017*. Rome: Food and Agriculture Organization of the United Nations. 168 pp.

Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, et al. 2007. The shuttle radar topography mission. *Reviews of Geophysics* 45: 1–33. https://doi.org/10.1029/2005RG000183.

Franco PM, Gine RS, Richard DL, Robert DF, Craig J, Tomas H, Eivin R. 2018. Livestock depredation by wild carnivores in the Eastern Serengeti Ecosystem, Tanzania. *International Journal of Biodiversity and Conservation* 10: 122–130. https://doi.org/10.5897/ijbc2017.1165.

Gazzola A, Bertelli I, Avanzinelli E, Tolosano A, Bertotto P, Apollonio M. 2005. Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology* 266: 205–213. https://doi.org/10.1017/S0952836905006801.

Graham K, Beckerman AP, Thirgood S. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159–171. https://doi.org/10.1016/j.biocon.2004.06.006.

Holmern T, Nyahongo J, Røskaft E. 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation* 135: 518–526. https://doi.org/10.1016/j.biocon.2006.10.049.

Iliopoulos Y, Sgardelis S, Koutis V, Savaris D. 2017. Wolf depredation on livestock in central Greece. *Mammal Research* 54: 11–22. https://doi.org/10.1007/bf03193133.

Kamler JF, Klare U, Macdonald DW. 2012. Seasonal diet and prey selection of black-backed jackals on a small-livestock farm in South Africa. *African Journal of Ecology* 50: 299–307. https://doi.org/10.1111/j.1365-2028.2012.01324.x.

Kerley GIH, Behrens KG, Carruthers J, Diemont M, du Plessis J, Minnie L, Richardson PRK, Somers MJ, Tambling CJ, Turpie J, et al. 2017. Livestock predation in South Africa: The need for and value of a scientific assessment. *South African Journal of Science* 113: 1–3. https://doi.org/10.17159/sajs.2017/a0198.

Khorozyan I, Ghoddousi A, Soofi M, Waltert M. 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation* 192: 268–275. https://doi.org/10.1016/j.biocon.2015.09.031.

Khorozyan I, Soofi M, Soufi M, Hamidi AK, Ghoddousi A, Waltert M. 2017. Effects of shepherds and dogs on livestock depredation by leopards (*Panthera pardus*) in north-eastern Iran. *PeerJ* 5: e3049. https://doi.org/10.7717/peerj.3049.

Khorozyan I, Waltert M. 2019. A framework of most effective practices in protecting human assets from predators. *Human Dimensions of Wildlife* 24: 380–394. https://doi.org/10.1080/10871209.2019.1619883.

Knowlton FF, Gese EM, Jaeger MM. 1999. Coyote depredation control: an interface between biology and management. *Journal of Range Management,* 52: 398–412. https://doi.org/10.2307/4003765.

Kolowski JM, Holekamp KE. 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation* 128: 529-541. https://doi.org/10.1016/j.biocon.2005.10.021.

Landa A, Gudvangen K, Swenson JE, Røskaft E. 1999. Factors associated with wolverine *Gulo gulo* predation on domestic sheep. *Journal of Applied Ecology* 36: 963–973. https://doi.org/10.1046/j.1365-2664.1999.00451.x.

Leighton GRM, Bishop JM, O'Riain MJ, Broadfield J, Meröndun J, Avery G, Avery DM, Serieys LEK. 2020. An integrated dietary assessment increases feeding event detection in an urban carnivore. *Urban Ecosystems* 23: 569–583. https://doi.org/10.1007/s11252-020-00946-y.

Letnic M, Ripple WJ, Isaac N. 2017. Large-scale responses of herbivore prey to canid predators and primary productivity. *Global Ecology and Biogeography* 26: 860–866. https://doi.org/10.1111/geb.12593.

Liu F, McShea W, Garshelis D, Zhu X, Wang D, Gong Je, Chen Y. 2009. Spatial distribution as a measure of conservation needs: an example with Asiatic black bears in south-western China. *Diversity and Distributions* 15: 649–659. https://doi.org/10.1111/j.1472-4642.2009.00571.x.

Loveridge AJ, Sousa LL, Seymour-Smith J, Hunt J, Coals P, O'Donnell H, Lindsey PA, Mandisodza-Chikerema R, Macdonald DW. 2020. Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biological Conservation* 244: e108504. https://doi.org/10.1016/j.biocon.2020.108504.

Marker LL, Mills MGL, MacDonald DW. 2003. Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology* 17: 1290–1298. https://doi.org/10.1046/j.1523-1739.2003.02077.x.

McManus JS, Dickman AJ, Gaynor D, Smuts BH, Macdonald DW. 2014. Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *Oryx* 49: 687–695. https://doi.org/10.1017/s0030605313001610.

Michler LM, Treydte AC, Hayat H, Lemke S. 2019. Marginalised herders: Social dynamics and natural resource use in the fragile environment of the Richtersveld National Park, South Africa. *Environmental Development* 29: 29–43. https://doi.org/10.1016/j.envdev.2018.12.001.

Middleton O, Svensson H, Scharlemann JPW, Faurby S, Sandom C, Pincheira-Donoso D. 2021. CarniDIET 1.0: A database of terrestrial carnivorous mammal diets. *Global Ecology and Biogeography* 30: 1175–1182. https://doi.org/10.1111/geb.13296.

Miller JRB, Stoner KJ, Cejtin MR, Meyer TK, Middleton AD, Schmitz OJ. 2016. Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildlife Society Bulletin* 40: 806–815. https://doi.org/10.1002/wsb.720.

Minnie L, Avenant NL, Drouilly M, Samuels I. 2018. Biology and ecology of black-backed jackal and caracal. In: Kerley GIH, Wilson S, Balfour D (eds.), *Livestock Predation and its Management in South Africa: a Scientific Assessment*. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela University. pp 178–204.

Minnie L, Gaylard A, Kerley GIH. 2016. Expression of Concern: Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology* 53: 1891–1891. https://doi.org/10.1111/1365-2664.12795.

Minnie L, Zalewski A, Zalewska H, Kerley GIH. 2018. Spatial variation in anthropogenic mortality induces a source-sink system in a hunted mesopredator. *Oecologia* 186: 939–951. https://doi.org/10.1007/s00442-018-4072-z.

Moritz M, Ritchey K, Kari S. 2011. The social context of herding contracts in the Far North Region of Cameroon. *The Journal of Modern African Studies* 49: 263–285. https://doi.org/10.1017/S0022278X11000048.

Mucina L, Rutherford MC. 2006. *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19*. Pretoria: South African National Biodiversity Institute. 801 pp.

Nattrass N, Conradie B. 2013. Jackal narratives and predator control in the Karoo, South Africa. Report no. 324 (CSSR Working Paper). University of Cape Town, Cape Town.

Nattrass N, Conradie B, Stephens J, Drouilly M. 2020. Culling recolonizing mesopredators increases livestock losses: Evidence from the South African Karoo. *Ambio* 49: 1222–1231. https://doi.org/10.1007/s13280-019-01260-4.

Odden J, Nilsen EB, Linnell JD. 2013. Density of wild prey modulates lynx kill rates on free-ranging domestic sheep. *PLoS ONE* 8: e79261. https://doi.org/10.1371/journal.pone.0079261.

Ogada MO, Woodroffe R, Oguge NO, Frank LG. 2003. Limiting depredation by African carnivores. *Conservation Biology* 17: 1521–1530. https://doi.org/10.1111/j.1523-1739.2003.00061.x.

Palmer BC, Conover MR, Frey SN. 2010. Replication of a 1970s study on domestic sheep losses to predators on Utah's summer rangelands. *Rangeland Ecology & Management* 63: 689–695. https://doi.org/10.2111/rem-d-09-00190.1.

Pinheiro JC, Bates DM. 2000. *Mixed Effects Models in S and S-Plus*. New York, Berlin, Heidelberg: Springer-Verlag. 528 pp.

RCoreTeam. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484. https://doi.org/10.1126/science.1241484.

Running S, Zhao M. 2019. MOD17A3HGF MODIS/Terra Net Primary Production gap-filled yearly L4 global 500 m SIN grid V006 [Data set]. NASA EOSDIS Land Processes DAAC.

Samuels MI. 2013. Pastoral mobility in a variable and spatially constrained South African environment. PhD thesis, University of Cape Town, South Africa.

Sangay T, Vernes K. 2008. Human-wildlife conflict in the Kingdom of Bhutan: Patterns of livestock predation by large mammalian carnivores. *Biological Conservation* 141: 1272–1282. https://doi.org/10.1016/j.biocon.2008.02.027.

Santini L, Isaac NJB, Ficetola GF. 2018. TetraDENSITY: A database of population density estimates in terrestrial vertebrates. *Global Ecology and Biogeography* 27: 787–791. https://doi.org/10.1111/geb.12756.

Sappington JM, Longshore KM, Thompson DB. 2007. Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71: 1419–1426. https://doi.org/10.2193/2005-723.

Schiess-Meier M, Ramsauer S, Gabanapelo T, König B. 2007. Livestock predation – Insights from problem animal control registers in Botswana. *Journal of Wildlife Management* 71: 1267–1274. https://doi.org/10.2193/2006-177.

Schurch MPE, McManus J, Goets S, Pardo LE, Gaynor D, Samuels I, Cupido C, Couldridge V, Smuts B. 2021. Wildlife-friendly livestock management promotes mammalian biodiversity recovery on a semi-arid Karoo farm in South Africa. *Frontiers in Conservation Science* 2: 1–15. https://doi.org/10.3389/fcosc.2021.652415

Skead CJ. 2007. *Historical Incidence of the Larger Land Mammals in the Broader Eastern Cape*. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University. 570 pp.

Skead CJ. 2011. *Historical Incidence of the Larger Land Mammals in the Broader Western and Northern Cape*. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University. 519 pp.

Somers MJ, Davies-Mostert H, Maruping-Mzileni N, Swanepoel L, Do Linh San E, Botha A, Tjelele J, Dumalisile L, Marnewick K, Tafani M, et al. 2018. Biology, ecology and interaction of other predators with livestock. In: Kerley GIH, Wilson SL, Balfour D (eds.), *Livestock Predation and its Management in South Africa: A Scientific Assessment.* Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela University. pp 228–254.

Thorn M, Green M, Dalerum F, Bateman PW, Scott DM. 2012. What drives human-carnivore conflict in the North West Province of South Africa? *Biological Conservation* 150: 23–32. https://doi.org/10.1016/j.biocon.2012.02.017.

Thorn M, Green M, Scott D, Marnewick K. 2013. Characteristics and determinants of human-carnivore conflict in South African farmland. *Biodiversity and Conservation* 22: 1715–1730. https://doi.org/10.1007/s10531-013-0508-2.

Treves A, Krofel M, McManus J. 2016. Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment* 14: 380–388. https://doi.org/10.1002/fee.1312.

Treves A, Naughton-Treves L. 2005. Evaluating lethal control in the management of human-wildlife conflict. In: Woodroffe R, Thirgood S, Rabinowitz A (eds.), *People and Wildlife: Conflict to Coexistance*. Cambridge: Cambridge University Press. pp 86–106.

Turpie JK, Babatopie A. 2018. The socio-economic impacts of livestock predation and its prevention in South Africa. In: Kerley GIH, Wilson SL, Balfour D (eds.), *Livestock Predation and its Management in South Africa: a Scientific Assessment*. Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela University. pp 53–81.

van Eeden LM, Eklund A, Miller JRB, Lopez-Bao JV, Chapron G, Cejtin MR, Crowther MS, Dickman CR, Frank J, Krofel M, et al. 2018. Carnivore conservation needs evidence-based livestock protection. *PLOS Biology* 16: e2005577. https://doi.org/10.1371/journal.pbio.2005577.

van Engelen VWP, Dijkshoorn JA. 2013. Global and national soils and terrain databases (SOTER). Procedures manual, v. 2.0. Report no. 2013/04 (ISRIC Report). Wageningen, The Netherlands.

van Niekerk HN. 2010. The cost of predation on small livestock in South Africa by medium-sized predators. MSc thesis, University of the Free State, South Africa.

van Sittert L. 1998. “Keeping the enemy at bay”: The extermination of wild Carnivora in the Cape Colony, 1889–1910. *Environmental History* 3: 333–356. https://doi.org/10.2307/3985183.

Verschueren S, Briers-Louw WD, Torres-Uribe C, Siyaya A, Marker L. 2020. Assessing human conflicts with carnivores in Namibia’s eastern communal conservancies. *Human Dimensions of Wildlife* 25: 452–467. https://doi.org/10.1080/10871209.2020.1758253.

Woodroffe R, Frank LG, Lindsey PA, ole Ranah SMK, Romañach S. 2007. Livestock husbandry as a tool for carnivore conservation in Africa’s community rangelands: a case-control study. *Biodiversity and Conservation* 16: 1245–1260. https://doi.org/10.1007/s10531-006-9124-8.

Yom-Tov Y, Ashkenazi S. 1995. Cattle predation by the golden jackal *Canis aureus* in the Golan Heights, Israel. *Biological Conservation* 73: 19–22. https://doi.org/10.1016/0006-3207(95)90051-9.

Zipkin EF, Inouye BD, Beissinger SR. 2019. Innovations in data integration for modeling populations. *Ecology* 100: e02713. https://doi.org/10.1002/ecy.2713.

Zipkin EF, Zylstra ER, Wright AD, Saunders SP, Finley AO, Dietze MC, Itter MS, Tingley MW. 2021. Addressing data integration challenges to link ecological processes across scales. *Frontiers in Ecology and the Environment* 19: 30–38. https://doi.org/10.1002/fee.2290.

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