RESEARCH ARTICLE

Scaling issues in the study of livestock depredation by carnivores

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Abstract

Context Many studies have documented the magnitude and socioecological drivers of livestock depredation, yet few have assessed how observations of depredation might vary with spatiotemporal scale. Understanding scaling relationships may allow for more accurate aggregation of observations collected across diverse extents and resolutions to better inform management actions.

Objectives Herein we examine how reported metrics of livestock depredation varied by spatial and temporal scale (extent and resolution) after controlling for other drivers of differences among studies.

Methods From 213 published studies we extracted conflict metrics (i.e., number of animals killed, number of attack incidents, and percent annual loss of stock) and regressed each against spatiotemporal extent (i.e., size of study area, duration of study) and resolution (i.e., minimum mapping unit, frequency of observations) while controlling for potential biases.

Results The number of attacks or animals killed was positively related to spatial and temporal extent whereas percent annual loss of stock declined with extent. Further, the effects of scaling variables were modified through interactions with other factors (e.g., human density) known to influence human-carnivore conflict. The data available for spatiotemporal resolution were too sparse to draw conclusions. While scaling relationships were generally linear, they became increasingly noisy at broader extents.

Conclusions Consistent with other ecological investigations, the scale of observation influenced the observed outcomes in human-carnivore conflict metrics. Authors should report the spatiotemporal dimensions of their observations to improve robust inference in comparative studies. Enhanced understanding of scaling relationships in human-carnivore conflict metrics should improve strategic allocation of resources to better mitigate future conflict.

Keywords Carnivore-human conflict · Extent · Livestock depredation · Resolution · Scale

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Introduction

Human-wildlife conflict, defined as adverse interactions between people and wildlife (Nyhus 2016), is one of the most pressing issues facing large mammal conservation today. Large carnivores pose a safety risk to humans (Packer et al. 2005, 2019). They also depredate livestock, with resultant financial costs for people (Van Niekerk et al. 2021a, b). Felids and canids are considered the greatest overall offenders (Ugarte et al. 2019), and human intolerance then becomes a threat to carnivores due to retaliatory killing (Inskip and Zimmermann 2009; Barua et al. 2013). Past research of human-carnivore conflict has focused on where and when conflict occurs (Inskip and Zimmermann 2009; Barua et al. 2013; van Niekerk et al. 2021a, b), financial and social costs (Dickman 2010; Kansky and Knight 2014; Lozano et al. 2019), techniques to reduce livestock depredation (Inskip and Zimmermann 2009; Miller et al. 2016; Eklund et al. 2017; van Eeden et al. 2018; Petracca et al. 2019), and measures to facilitate coexistence (Dickman et al. 2011). Numerous studies have also investigated which ecological drivers influence human-carnivore conflict. The relationship between depredation risk, land use, and human presence depends on the spatial resolution and extent at which the process is studied, although strength of covariate relationships is often highest at finer scales (Miller et al. 2015; Fowler et al. 2019). Risk generally increases closer to open areas where canids are the primary predator (Treves et al. 2011; Miller 2015), whereas it increases in the proximity of dense forests when felids are involved (Zarco-González et al. 2013; Miller 2015; Miller et al. 2015). Importantly, environmental and anthropogenic variables sometimes demonstrate nonlinear relationships with probability of depredation, as has been recorded with human population density, proportion of agricultural land, and distance from roads, villages, and open vegetation (Miller et al. 2015; Fowler et al. 2019). Thus, management of human-carnivore conflict would benefit by assimilating information across disparate studies. Nevertheless, authors have repeatedly pointed to the absence of attention to potential scaling issues when attempting to draw inference on carnivore conflict across studies (Nyhus 2016; Montgomery et al. 2018). Despite several hundred studies of human-carnivore conflict having been published since the 1990s (Ugarte et al. 2019; Khorozyan and

Waltert 2021), potential scaling relationships remain unresolved. Uncovering the relationship between scale and human-carnivore conflict metrics is needed for more robust aggregation of observations collected at fine spatial scales, and across diverse temporal extents and resolutions, to inform policies and management actions undertaken at larger spatiotemporal scales (Iannone et al. 2016).

Improper consideration of the scale-dependent nature of ecological processes may hinder predictive capacity for targeted conservation action (Wiens 1989; Menge and Olson 1990; Levin 1992). Predator–prey dynamics, as well as patterns of human-wildlife conflict, depend on whether they are observed at relatively fine or broad scales (Odden et al. 2008, 2013; Chetri et al. 2019; Buchholtz et al. 2020). Without consideration of scale, inferences regarding conflict hotspots, magnitude, and mitigation effectiveness may well be muddied, interfering with effective conservation action. Spatiotemporal context matters given that ecological systems are the product of multiple processes operating at different hierarchical levels, e.g., geomorphological, climatic, and anthropogenic processes (Kotliar and Wiens 1990; Turner and Gardner 2015). Indeed, the outcomes of every natural phenomenon such as disturbance (Hamer and Hill 2000; Dumbrell et al. 2008), habitat selection (Orians and Wittenberger 1991; Mayor et al. 2009), animal movement (Frair et al. 2005), and interspecific interactions (Fauchald et al. 2000) depend fundamentally on the spatiotemporal scales at which they are considered.

It is possible to identify characteristic scales at which processes operate, resulting in generally repetitious patterns to emerge at regular time intervals (Loucks 1970; Wu and Loucks 1995). Moreover, it is possible to map a scaling relationship that enables more effective comparison of outcomes measured on different scales as well as extrapolation among scales of observation (Newman et al. 2019). Many ecological studies have demonstrated non-linear relationships between scale and observation (Wiens 1989; Rastetter et al. 1992; Wu et al. 2002; Wu 2004; Mayor and Schaefer 2005), challenging the comparison of observations made at one scale to those made at other scales. Generally, making predictions is most difficult at intermediate scales, where top-down and bottom-up factors interact (Newman et al. 2019). Moreover, patterns of correlation between two variables may

only be evident at one particular scale, as has been observed with environmental conditions and vegetation composition (Reed et al. 1993; Schaefer and Messier 1995). Fundamentally, scale decomposes into extent and resolution; extent is the size (spatial) or duration (temporal) of a study, whereas resolution is the minimum mapping unit or sampling unit expressed in terms of space or time (Turner and Gardner 2015). Generally speaking, decreasing resolution while holding extent constant results in a clearer pattern between two variables because fine-scale variations in the process of interest are averaged away over larger resolutions (Reed et al. 1993; Wu et al. 2000). By contrast, the ramifications of changing extent while holding resolution constant are less clear because more heterogeneity both from the variable of interest and the surrounding environment will be included (Reed et al. 1993; Wu et al. 2002; Wu 2004). Typically, increases in extent often accompany, perhaps by necessity, increases in resolution.

While the relationship between scaling dimensions and human-carnivore conflict metrics has been assessed for single species or specific regions, such as brown bear (*Ursus arctos*) in the French Pyrenees (Gastineau et al. 2019; Wells et al. 2019), it is unknown how robust such scaling relationships are globally or across other species assemblages. With broader-scale and multi-species considerations, we would expect non-linear relationships and interactions among drivers to become important, as well as greater variation in the magnitude of conflicts observed and as a result, predictions of conflict to become more challenging (Wu et al. 2000; Baruch-Mordo et al. 2008; Wells et al. 2019). For instance, uncertainty regarding the presence of conflict hotspots, defined as locations with disproportionately frequent attacks due to surrounding landscape features (Miller 2015), is greater at finer versus broader spatial extents, which could reflect differences in sizes of grazing pastures or carnivore habitat quality (Baruch-Mordo et al. 2008; Gastineau et al. 2019). Locations of hotspots remain fairly stable within a year and across longer study durations, although uncertainty may be high in the numbers of animals killed among years (Baruch-Mordo et al. 2008; Gastineau et al. 2019). Total numbers of animals killed has also proven more unpredictable with increasing spatial extent, which might reflect heterogeneity in spatial associations of carnivores with livestock across the landscape (Wells et al.

2019). Determining whether mismatches in scale confound detection of patterns (Montgomery et al. 2018), or lead to biased insights, should enhance our ability to effectively assess and implement management techniques aimed at reducing livestock deaths by predators.

Herein we explicitly investigate how common measures of conflict, as reported in the published literature, vary globally with increasing spatial and temporal scale. To achieve this, we conducted a literature review of existing livestock depredation data from carnivores worldwide, restricting our search to felids, canids, ursids, and mustelids. From this body of literature, we extracted conflict metrics and recorded the spatiotemporal scale of observation. Ultimately, we regressed these metrics against spatial or temporal extent and resolution while controlling for human population density and body mass of the largest carnivore involved in human-wildlife conflict, given evidence that these variables are positively correlated with conflict (Woodroffe 2000; Ugarte et al. 2019).

Materials and Methods

We searched Web of Science, from 1985 through January 2022, for peer-reviewed papers reporting livestock loss to carnivores (Online Resource 1). Search criteria included Title = (carnivore* OR mammal* OR predator* OR felid* OR canid* OR ursid* OR hyaena OR lion* OR hyena* OR bear* OR jaguar* OR leopard* OR tiger* OR wolf OR wolves OR wild dog* OR lynx OR cougar* OR puma* OR coyote*) AND Title = (depredation OR livestock OR conflict* OR human* landscape OR human-wildlife conflict OR human-carnivore conflict), which resulted in 1,009 papers. We restricted results to the subject areas of Ecology, Zoology, Biodiversity Conservation, Environmental Sciences, Veterinary Sciences, Multidisciplinary Sciences, Genetics Heredity, Behavioral Sciences, Geography Physical, Biology, Agriculture Dairy Animal Science, Geosciences Multidisciplinary, Environmental Studies, Sociology, Evolutionary Biology, and Geography. From a total of 888 papers returned by that search, we excluded papers that did not distinguish livestock depredation from other instances of conflict (e.g., raiding trash cans, behaving aggressively toward humans or pets, human injuries), literature reviews in lieu of original

research, and those focused on predator diet composition rather than conflict rates. Lastly, to be included in this study, authors needed to have reported metrics of depredation that could be converted into a common currency across studies as described below.

There were three commonly reported currencies of predation rate: *percent annual loss of stock* (hereafter, %loss), *total number of attack incidents across the entire study* (#attacks), and *total number of animals killed across the entire study* (#kills) (Mishra 1997; Conner et al. 1998; Kaartinen et al. 2009; Thorn et al. 2012; Amador-Alcalá et al. 2013; Guerisoli et al. 2017). Percent annual loss was the proportion of animals killed divided into the length of the study period. Number of attacks was the number of occasions where predators made depredation attempts as defined by the authors. Number of animals killed referred to the total count of depredated livestock. The most common prey items were cattle (*Bos primigenius f. taurus*), sheep (*Ovis orientalis f. aries*), and goats (*Capra aegagrus f. hircus*), although horses (*Equus ferus f. caballus*), donkeys (*Equus africanus f. asinus*), and pigs (*Sus scrofa f. domestica*) occurred too, among others. We included all papers that provided the necessary data to calculate these metrics when they were not directly reported (Online Resource 2). Calculating %loss necessitated data on the total number of animals killed together with the total size of the herd, whereas the other metrics required knowledge of the total number of either attack incidents or animals killed. In addition to recording depredation data, we noted the spatial and temporal extents and resolutions at which data were collected. Spatial *extent* was defined as the total study area in km^2, while *resolution* (km^2) was the finest sampling unit at which depredation data were recorded, often at the level of individual farms, pastures, or management units. Temporal extent was defined as the study duration in years, while resolution defined the regular intervals (typically months) at which data were recorded within the study.

We predicted that #kills and #attacks would increase linearly with both space and time, while plateauing at the broadest spatial scales. This latter expectation was based on the nature of herding livestock within concentrated areas, leaving surrounding regions with few individuals to be predated (Stahl et al. 2001; Rosas-Rosas et al. 2008). Moreover, we predicted that while %loss would not change on

average across years (because it represents an annual proportion), it too should saturate or decrease at broader spatial scales. The latter expectation is predicated on the assumption that there would be more livestock overall on the landscape given larger spatial extents yet a proportionally smaller number of individuals being killed due to the uneven distribution of attacks across the landscape (Stahl et al. 2001; Gastineau et al. 2019). Additionally, scaling laws might be affected by other determinants. The relationship between temporal duration and observations of conflict might depend on the size of a study area (i.e., temporal x spatial extent interaction) due to differences in land use, number of livestock, and wild prey availability, among other factors (Odden et al. 2013; Chetri et al. 2019; Mukeka et al. 2019; Wilkinson et al. 2020). Higher human densities may correspond to higher levels of conflict where associated with greater concentrations of livestock (Mukeka et al. 2019). And larger-bodied predators might kill more livestock than smaller predators (Ugarte et al. 2019), with their differing patterns of space use affecting scaling relationships across space and time.

We used multivariate regression models to explore how depredation observations might vary by spatiotemporal extent (i.e., study area size and study duration) and resolution while controlling for predator body size (Ugarte et al. 2019) and human population density (Woodroffe 2000; Harcourt et al. 2001; Ogada et al. 2003). For each reported study site, we extracted human population density (people/km^2) using Google Earth Engine (https://sedac.ciesin.columbia.edu/) (Woodroffe 2000; Harcourt et al. 2001; Ogada et al. 2003). Although studies reported depredating species without reporting specific body sizes, we based adult masses on (Jones et al. 2009) and lumped predator species into body size categories as "large" (> 100 kg; ursids, tigers [*Panthera tigris*], and lions [*Panthera leo*]), "medium" (50–100 kg; smaller felids and hyaenids), and "small" (< 50 kg; primarily canids and lynx [*Lynx lynx*]). We included the largest size class (as reported by authors) as an indicator category when fitting regression models. Continuous explanatory variables (population density and scale variables) were centered and scaled prior to model fitting (Breiman and Friedman 1997). The dependent variables #attacks and #kills were log-transformed to achieve a normal distribution, and models were fit using a gaussian distribution of error.

The response %loss did not require transformation a priori, but a disproportionately high number of observations at low %loss necessitated using a gamma distribution with log link. Lastly, we included a random effect of continent to account for global ecological and socioeconomic differences in systems of human-wildlife interactions (Lozano et al. 2019). We fit models using the lmerTest package in R and extracted R^2 values using the MuMIn package. Figures were created using the ggeffects package.

The most informative set of covariates was identified using Akaike's Information Criterion (AIC; Akaike 1987) using the AICcmodavg package, with model selection uncertainty identified where $\Delta AICc < 2$ (Burnham and Anderson 2002). All models, including the null model, controlled for the effects of carnivore body size (categorical covariate) and human density (continuous covariate; Online Resource 3). Candidate models individually included spatial extent, temporal extent, and combinations of both spatial and temporal extent. Models further compared spatiotemporal covariates as either linear or quadratic terms to allow relationships to plateau or change direction with increasing scale. Lastly, some models included hypothesized two-way interactions between spatiotemporal variables and the two control variables (carnivore body size and human density) to assess whether scaling relationships were dependent on these factors. Sample sizes precluded model selection for resolution-related metrics given 16–17 (spatial) and 37–77 (temporal) data points per conflict metric.

Results

From 606 published articles meeting our search criteria, we were able to sufficiently infer data on spatiotemporal scale and conflict metrics from 213 (35%), with 62 (29%) to 111 (52%) of those reporting one of our specific response metrics (Table 1). These represented five continents involving 17 carnivore species (Fig. 1). Forty-six percent of studies involved carnivores over 100 kg, and 36% focused on species less than 50 kg. Studies reporting %loss and #kills were more common in Asia (35% and 41%, respectively) while #attacks was more common in North America (35%). Ninety-five studies measured loss of cattle, whereas sheep and goats were considered in 103 studies. The remaining studies only included less common species (e.g. horse, pig) or pooled total loss without providing frequency of occurrence per species. In terms of spatiotemporal metrics, studies spanned spatial extents 10–8,500,000 km² and 0.06–76 years (Table 1).

Top models across all three conflict metrics included spatial or temporal variables, showing clear improvement over the null model with the inclusion of scaling effects ($\Delta AICc$ over null model ≥ 5.2; Table 2). The top models for #attacks and #kills each included temporal extent, while the top model for %loss included both spatial and temporal extent (Table 2; Online Resource 3). The continental random effect did not explain any variation in the models.

Greater percent annual loss was associated with finer spatial and temporal extent. Partial slopes indicated a decreasing trend between %loss and increasing spatial (Fig. 2) and temporal (Fig. 3) extent. Scaling variables were important in terms of AIC, adding considerable information over the null model ($\Delta AICc = 5.2$–102.0 over the null depending on dependent covariate), but their estimated slopes were noisy and thus lacked statistical significance at the $P < 0.05$ level. Log(#kills) was greatest for species having body mass in the 50–100 kg range, being significantly greater than the largest body mass category (1.63 ± 0.58 SE; Table 3), and increased with greater temporal extent, with the steepest slope observed for mid-sized carnivores (2.24 ± 0.60 SE; Fig. 3). Greater log(#attacks) was associated with increasing temporal extent (0.68 ± 0.22 SE), notably so in areas of higher human population density (0.91 ± 0.37 SE; Fig. 3),

Table 1 Summary of conflict measures and spatial and temporal scale

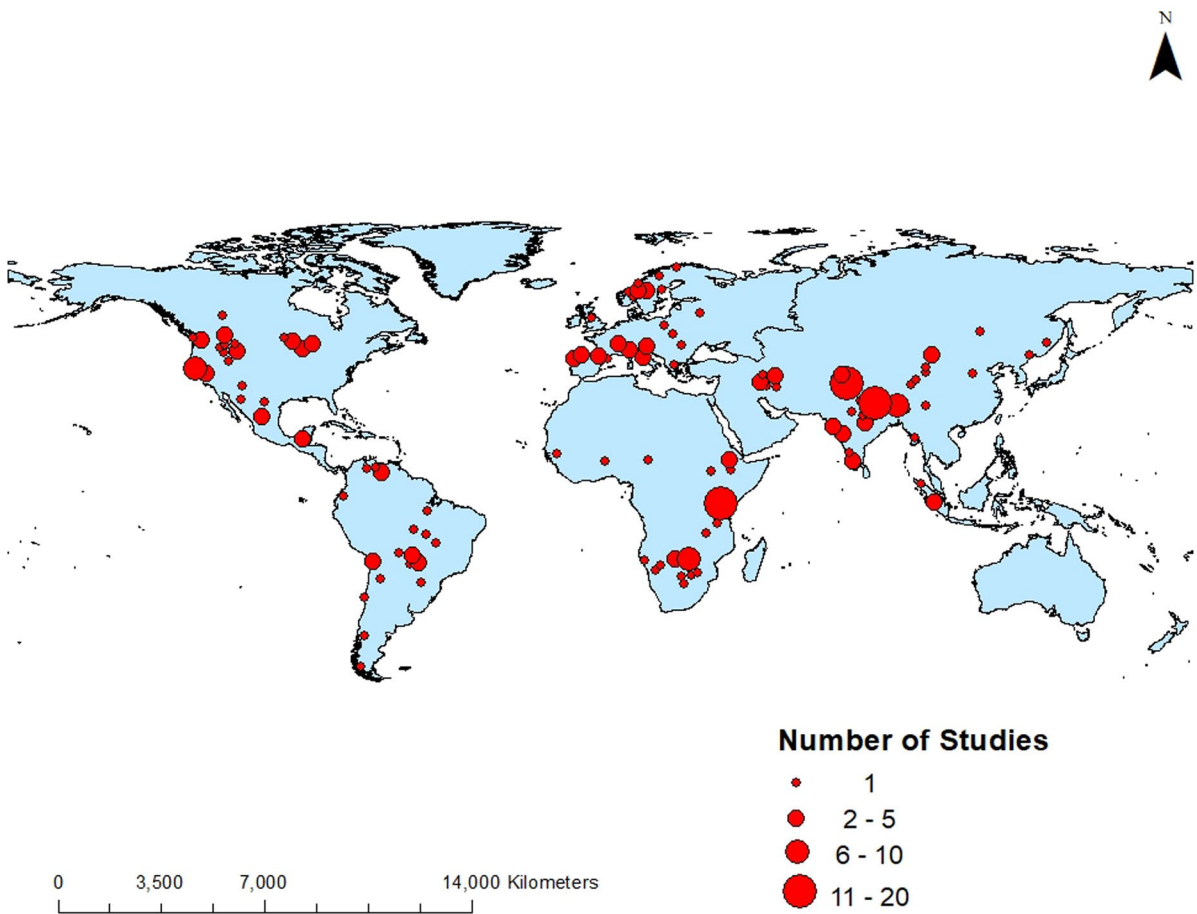| Conflict measure	Number of studies	Spatial extent		Temporal extent	
		Mean ± SD (km²)	Range	Mean ± SD	Range
%loss	76	22,278 ± 77,111	20–440,000	4 ± 3 years	0.25–14
#kills	111	141,698 ± 833,721 km²	10–8,500,000	6 ± 8 years	0.06–55
#attacks	62	125,329 ± 314,748 km²	22–1,953,162	11 ± 12 years	0.17–76

Fig. 1 Global distribution of studies assessing livestock depredation by carnivores from a literature review of 213 peer-reviewed articles. Circle size demonstrates the local density of studies, specifically the number of studies whose location centers fell within a 100-km radius

indicating that more attack incidents occurred across longer time periods at higher versus lower human densities. Ultimately, residuals were normally distributed across the top models for all metrics, indicating appropriate model fit (Online Resource 3).

Discussion

Ecologists have long demonstrated how ecological patterns and processes can change over space and time, and that the window through which we observe outcomes affects the inferences gained (Turner and Gardner 2015). Despite calls for more explicit consideration of scale from authors attempting to synthesize the human-carnivore conflict literature (Nyhus 2016; Montgomery et al. 2018), to our knowledge this is the first attempt to comprehensively investigate globally-relevant scaling relationships. Using three common metrics depicting severity of conflict (percent annual loss of stock, number of animals killed, and number of attack incidents), we observed strong support for models including the effects of spatial or temporal extent of the study, as well as temporal resolution, indicating that the spatiotemporal scale of observation is important to the observed conflict outcomes. Although these effects were largely linear, which makes for easier interpretation of scaling relationships, in all cases scaling effects were modulated through interactions either with each other (e.g., spatial×temporal extent) or in combination with carnivore body size or human population density. Given

Table 2 AIC model comparison of candidate models predicting percent annual loss (%loss; N=76), number of animals killed (#kills; N=111), and number of depredation incidents (#attacks; N=62)

Model description	Main effects				Interactions					K	ΔAIC		
	Spatial extent (SE)	Temporal extent (TE)	Human density (HD)	Carnivore mass (CM)	SE x TE	SE x HD	SE x CM	TE x HD	TE x CM		%loss	#kills	#attacks
Spatial×temporal	x	x	x	x	x					8	**0.0**	10.8	**1.8**
Full linear	x	x	x	x	x	x	x			11	**1.5**	12.7	–
Spatial linear	x		x	x						6	5.7	14.2	7.1
Spatial×HD	x		x	x		x				7	5.8	16.2	9.5
Spatial nonlinear	x, x²		x	x						7	7.2	13.9	4.2
Full nonlinear	x, x²	x, x²	x, x²	x	x	x	x			14	7.8	14.0	–
Spatial×CM	x		x	x			x			8	8.9	14.5	9.4
Spatial nonlinear+HD nonlinear	x, x²		x, x²	x						8	9.6	14.2	**0.1**
Temporal linear		x	x	x						6	97.0	8.4	3.0
Temporal nonlinear		x, x²	x	x						7	98.0	5.9	2.4
Temporal×HD		x	x	x				x		7	99.0	9.2	**0.0**
Temporal×CM		x	x	x					x	8	99.0	**0.0**	8.1
Temp. nonlinear+HD nonlinear		x, x²	x, x²	x						8	100.4	6.4	**0.4**
Null			x	x						5	102.0	13.3	5.2

Main effects and interactions included in each model are indicated, along with linear (x) or quadratic fits as appropriate. Total number of parameters (K) is shown along with ΔAIC values for each model, with models contributing to model selection uncertainty indicated in **bold**

Fig. 2 Predicted relationships between spatial extent and **a** %loss, **b** log(#kills), and **c** log(#attacks) from the single top models. The legends in panels **a** and **b** represent temporal extent, given that this variable was included in an interaction with spatial extent in the top model
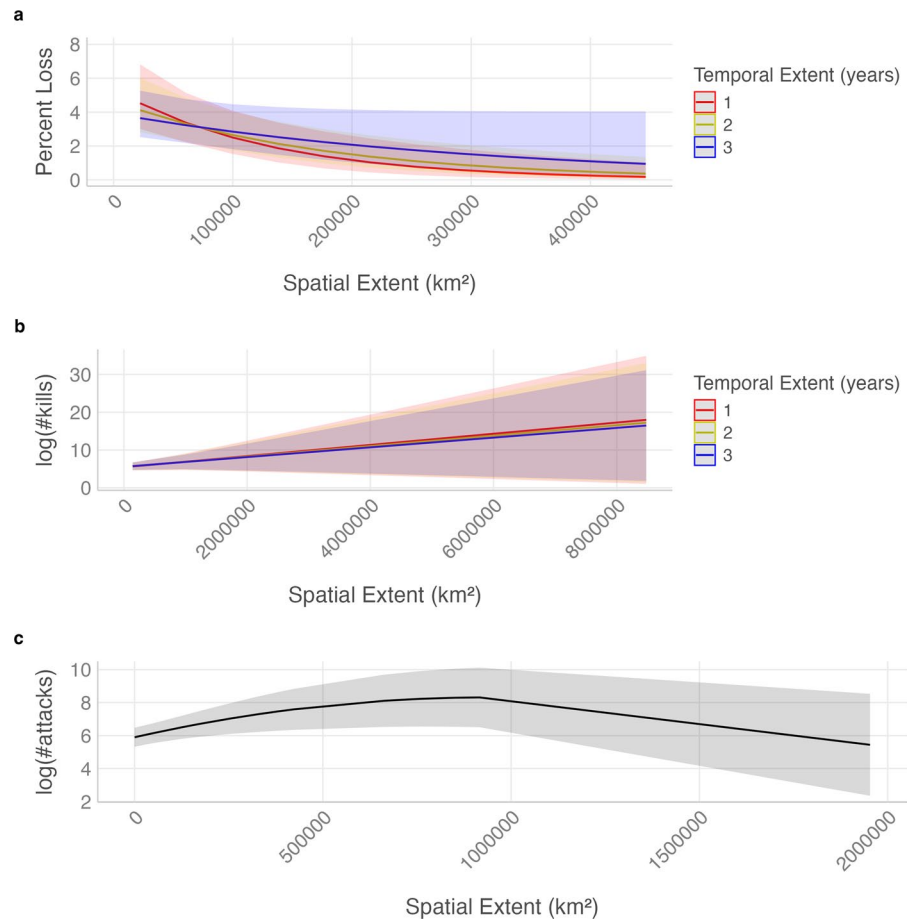
highly noisy relationships, stemming in part from the necessary inclusion of multiple livestock and predator types in the same model to achieve viable sample sizes (and using the largest reported body size from the suite of potential predators in a study), imprecise specifications of conflict metrics (deduced from reports), and incomplete reporting of scale dimensions by study authors, it was not surprising that the estimated effects for scaling relationships mostly failed to achieve statistical significance. Nevertheless, the scaling trends were compelling, consistent overall with our expectations, and present ramifications for management as outlined below.

Knowledge of the severity of human-carnivore conflict greatly enhances the ability of managers to efficiently allocate resources where they are most needed. When estimates of livestock depredation are required at a given extent (e.g., township, province), but data are only available at an alternative scale (e.g., farm, ranch), the curves outlined herein may be useful

in extrapolating patterns to policy-relevant scales. Rather than simply linearly extrapolating, which fails to account for relevant covariates influencing the scaling relationship (e.g., human density, carnivore body mass), as well as how conflict patterns differ depending on how they are measured (e.g., #kills versus #attacks), our models may be used to account for nonlinear trends and interacting covariate effects. This process is vital to ensure patterns are correctly predicted at the new scale, which will vary based on how patchy or concentrated depredation observations are. Moreover, the prediction uncertainty of our curves, and therefore range of potential loss, can help managers determine the appropriate mitigation techniques and allocate resources based on varying levels of risk. The same conclusions regarding prediction accuracy hold true within the temporal dimension as well.

The positive relationship observed between spatiotemporal extent and number of observed events (attack incidents or animals killed) was expected

Fig. 3 Predicted relationships between temporal extent and **a** %loss, **b** log(#kills), and **c** log(#attacks) from the single top models. The legends in panels (**b**) and (**c**) represent carnivore mass and human density, respectively, given that these variables were included in an interaction with temporal extent in the top model
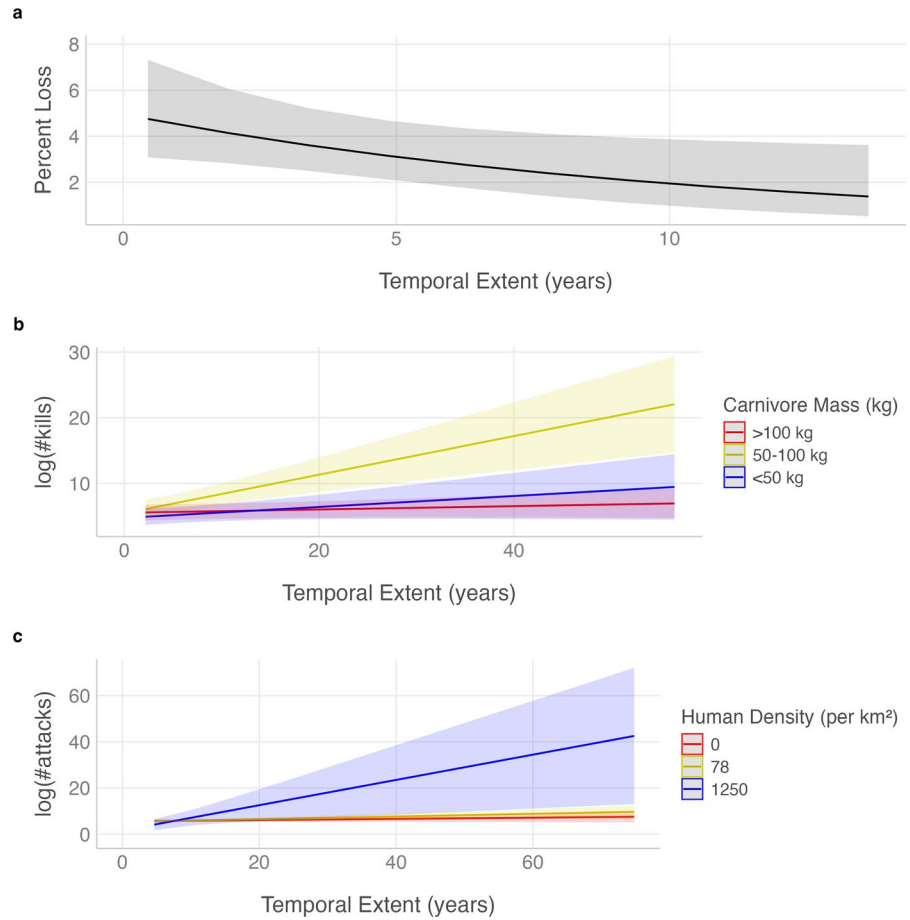

Table 3 Parameter estimates (β) with standard errors (SE) for the single most parsimonious models predicting the three metrics of conflict (percent annual loss [%loss], number of animals killed [#kills], and number of attack incidents [#attacks])

	%loss (N = 76)		#kills (N = 111)		#attacks (N = 62)	
	Estimate	Standard Error	Estimate	Standard Error	Estimate	Standard Error
Intercept	1.28	0.20	5.69	0.59	5.97	0.29
Human Density	− 0.06	0.16	− 0.09	0.15	0.22	0.26
Carnivore Mass (50–100 kg)	− 0.11	0.32	1.63	0.58*	− 0.26	0.62
Carnivore Mass (< 50 kg)	− 0.11	0.31	− 0.41	0.35	− 0.31	0.41
Spatial extent	− 0.23	0.15	–	–	–	–
Temporal extent	− 0.28	0.15	0.21	0.17	0.68	0.22*
Spatial × Temporal	0.44	0.36	–	–	–	–
Carnivore Mass (50–100 kg) × Temporal extent	–	–	2.24	0.60*	–	–
Carnivore Mass (< 50 kg) × Temporal extent	–	–	0.49	0.42	–	–
Human Density × Temporal extent	–	–	–	–	0.91	0.37*

Except for the categorical carnivore body mass, all covariates were centered and scaled prior to model fitting. Prior to model fitting #kills and #attacks were log-transformed. Those variables whose confidence intervals exclude zero are indicated by *. Dashes (–) indicate the variable was not included in any competing models. The conditional R^2 values are 0.23 (%loss), 0.52 (#kills), and 0.21 (#attacks)

given that broader extents will likely contain greater numbers of livestock and predators while longer time periods put animals at greater cumulative risk of a predation encounter (Baruch-Mordo et al. 2008; Gastineau et al. 2019; Wells et al. 2019). The potential non-linear response observed for number of attack incidents, which peaked at intermediate spatiotemporal scales, likely stemmed from ever-greater landscape heterogeneity with further increases in scale due to human infrastructure and population size, carnivore species, number of livestock, and patchiness of livestock operations and carnivore habitat (Kaczensky 1999; Wilkinson et al. 2020; Zimmermann et al. 2021; Göttert and Starik 2022). The negative association between spatiotemporal extent and percent annual loss of stock could in part be attributed to the nature of herding livestock. For example, within a fine extent (e.g., an individual ranch), there could be a single herd and therefore a higher %loss than if that proportion was quantified across an entire country where vast areas of land may hold no livestock (Stahl et al. 2001; Rosas-Rosas et al. 2008). Moreover, %loss decreased with longer time periods, which may be due to our methodology. Where not explicitly given, %loss was determined by first dividing total numbers of animals killed across the entire period into average herd size across the years, and then into the study duration. This approach assumed herd size remained constant over time, which may not hold true (Patterson et al. 2004). Alternatively, the negative trend may reflect differences in husbandry or the ecological state, such as in predator richness or wild prey abundance, over time (Guerisoli et al. 2017; Suryawanshi et al. 2017; Chaka et al. 2021). Also, there may be pulses in livestock loss, with stronger signals evident at shorter time scales.

The number of depredation observations is generally more variable at increasingly broad resolutions due to heterogeneity within the landscape, and because variance of counts increases with the mean. Such heterogeneity is in part caused by natural geographic variation, but also heavily influenced by human presence and land use (Acharya et al. 2017; Wilkinson et al. 2020). These factors alter habitat composition and arrangement (Acharya et al. 2017), wild prey availability (Odden et al. 2013), distance to human infrastructure (Sharma et al. 2020), and livestock accessibility to predators (Kuiper et al. 2022), features that in turn influence the direction

and magnitude of conflict depending on the predator species involved and husbandry practices in place (Rostro-García et al. 2016; Khorozyan and Waltert 2021). By contrast, relationships between conflict and its drivers are generally more precise and predictable at finer spatial grains (Miller et al. 2015; Fowler et al. 2019), and at finer temporal resolutions that correspond to seasonal differences (e.g., spring, summer, fall, and winter; wet versus dry) (Patterson et al. 2004; Sangay and Vernes 2008; Petracca et al. 2019). The lack of proper specification of resolution in most studies stymied our ability to detect meaningful patterns. Moreover, although there are ecological grounds to suspect heteroscedasticity in the data based on the biophysical landscape, husbandry practices, and predator species involved (Miller 2015; Miller et al. 2015; Broekhuis et al. 2017), the low sample sizes prohibited us from exploring that in any great detail.

We attempted to control for variation in human density when illuminating scaling relationships, yet at a global level human density does not necessarily equate to more livestock depredated because effective management practices (e.g., well-maintained fencing and livestock guarding) might be in place or livestock densities could be lower (Ogada et al. 2003; Graham et al. 2005; Weise et al. 2018; Khanal et al. 2020). Predator populations are also generally lower in areas with high human density (Woodroffe 2000), although most conflict occurs near protected areas where large carnivores remain at higher numbers than the surrounding matrix (Madden 2004; Nyhus 2016). Thus, human density might explain more variation as a covariate if this study were repeated at finer scales in more homogeneous conditions, for instance within one country, county, or region. Nevertheless, it is clear from our scaling relationships that livestock depredation, specifically #attacks, increases over time at high human densities and this should be considered when drafting long-term management plans.

We further attempted to control for predator body size by including a categorical covariate that adjusted the slope to account for the largest species involved (as reported by authors) given that some studies pool livestock killed across all predator species. However, the largest carnivore might not necessarily be the most damaging. For instance, in parts of Africa, lions are frequently blamed for livestock deaths even though smaller-bodied hyenas (*Crocuta crocuta*) are

often the primary depredators (Kissui et al. 2019). The same holds true in Nepal, where snow leopards (*Uncia uncia*) kill more yak (*Bos grunniens*) and horses than the larger brown bear (Chetri et al. 2019). Within Bhutan, leopards (*Panthera pardus*) often take more animals than tigers (Sangay and Vernes 2008). Such examples may explain why carnivore body mass in the 50–100 kg range displayed a significant trend with #kills as compared to predators over 100 kg. Splitting depredation by predator and livestock species would create a more robust picture of scaling relations between conflict and body mass, but again to investigate patterns in spatiotemporal scaling relationships by predator species requires that more studies effectively report their scale of investigation.

In addition to human density and predator species, wild prey availability can influence severity of livestock depredation as well (Khorozyan et al. 2015; Suryawanshi et al. 2017; Janeiro-Otero et al. 2020). We were unable to consider this variable in our analysis as few studies reported it, likely due to the difficulty of measuring wild ungulate abundances and defining what is "available" to a given predator species (Elbroch et al. 2016; Ghoddousi et al. 2016). The ability of a carnivore to switch between different prey species, including between livestock and wild ungulates, depends on its numerical and functional responses (Murdoch 1969). Theoretically, if a preferred wild prey item increases, yet the predator population does not increase as a result, livestock depredation will decrease as predators switch their focus to target wild ungulate species (apparent facilitation) (Holt 1977; Long et al. 2012; Suryawanshi et al. 2017). On the contrary, if predator populations increase in response to increasing wild prey abundance, livestock depredation might initially increase and reach an asymptote (apparent competition, type II functional response), or increase followed by subsequent decline (apparent facilitation, type III functional response) (Holling 1959; Abrams and Matsuda 1996; Suryawanshi et al. 2017). The correlation between livestock depredation and wild prey availability will therefore depend on the biology of the predator species and the context of the study system, further impacting spatiotemporal scaling relationships and likely causing some of the uncertainty observed herein.

Despite a robust model selection exercise, and the detection of some statistically significant relationships, wide variation in results especially at broader scales warrants further research on drivers of the unexplained variation. Specifically, husbandry type could be incorporated in a common currency of comparison (van Eeden et al. 2018; Khorozyan and Waltert 2021) provided it is consistently reported. Moreover, the relationship between conflict and scale may prove more informative for individual carnivore species because drivers of risk, specifically biophysical features, vary across predator species (Miller 2015). For example, extrapolating the number of livestock killed within enclosures set in relatively open landscapes to a regional level would underestimate the magnitude of risk if other livestock enclosures were set in more densely vegetated areas, ideal for stalking predators, or implemented weaker fencing (Broekhuis et al. 2017; Weise et al. 2018). One approach by which to consider these interplaying factors, and to decipher the underlying relationship between two variables regardless of confounding variables, is by using mixed-effects models (Iannone et al. 2016). Random effects can account for unexplained spatial heterogeneity across the region where extrapolation is warranted, including when the confounding variable is unknown, by using proxies that represent generally homogeneous conditions (Iannone et al. 2016). We used continent as a random effect, though this variable did not account for any of the variation in the models across our metrics, suggesting that finer-scale factors like habitat type might account for additional heterogeneity. Such an analysis however would warrant larger sample sizes across each level of the random effect than we were able to achieve herein.

We also note that the range of our scale variables was extensive, particularly for spatial extent. The median of spatial extent was no larger than 2000 km^2 for %loss and #kills, with less than five outlying observations ranging up to 8,500,000. For #attacks, the median was 5,500 km^2 with less than ten outlying observations ranging up to 2,000,000 km^2. We accounted for this uneven distribution of data by centering and scaling our explanatory variables to improve model robustness. We reiterate here the importance of clearly specifying the spatial and temporal dimensions of a study, and comparable conflict metrics, given our inability to extract such information from 65% of the published literature. This lack of

data challenges interpreting and effectively contextualizing most of the carnivore conflict literature. Moreover, there was a strong bias in the published cases, with most occurring in Southeast Asia and Equatorial Africa. Abundance of studies generally reflects patterns in livestock abundance (https://www.visualcapitalist.com/cp/mapped-global-livestock-distribution-and-density/) and human population density (https://luminocity3d.org/WorldPopDen/#2/39.0/9.1), most notably in Southeast Asia. By contrast, the northwestern U.S. and southwestern Canada generally contain moderate livestock abundance, low human population densities, and moderate-high rates of conflict publications. Numbers of studies thus largely reflect research-intensive regions driven by universities or governments.

Our findings indicate that observations of livestock depredation by carnivores are scale-dependent to some extent at a global level, specifically regarding study duration, and exhibit generally linear albeit noisy relationships, depending on how conflict is measured. Understanding scaling relationships informs aggregations of observations collected across different extents and resolutions, as well as where aggregation might be unfeasible due to high extrapolation uncertainty (Iannone et al. 2016; Newman et al. 2019). Thus, fertile areas of research to build on these results include elucidating which drivers significantly influence depredation at given scales, and how these relationships in turn affect conflict and associated mitigation at lower or higher levels of the system (Nyhus 2016; Montgomery et al. 2018; Fowler et al. 2019). Given that few studies have assessed scaling relationships for carnivore conflict within a system (Gastineau et al. 2019; Wells et al. 2019), and until now none have quantified scaling relationships across diverse socioecological contexts, it is clear that greater effort is needed to reveal the underlying drivers of scaling laws, clarify patterns, and elucidate which drivers are relevant to predicting conflict regardless of the spatiotemporal scale of data collection (Wu 2004).

Carnivore management in general, and management of human-carnivore conflict in particular, is itself a multi-dimensional endeavor requiring broad-scale policies and fine-scale regulations, actions, and monitoring (Carter and Linnell 2016). Measures taken to reduce the impacts of carnivores include but are not limited to financial incentives and compensation, technical changes in livestock husbandry (e.g., use of guard dogs or mobile fencing), enhancement or restoration of wild prey, regulated hunting, and educational campaigns (Carter and Linnell 2016). The observed outcome of these measures will certainly be scale-dependent to some degree, but their overall efficacy will depend fundamentally on the effective integration of diverse stakeholders and use of participatory decision-making practices—aspects beyond the scope of our investigation. That said, scientific information is more likely to be used by decision-makers when deemed salient with respect to the spatial, temporal, and jurisdictional scales of the problem at hand (Gordon et al. 2016). By extension, a major hindrance of the current carnivore-conflict literature is the risk that research will be ignored when rendering policy-decisions or selecting mitigation actions because of the inability to understand the research implications considering the scales at which decisions are made. Our contribution is to provide some means of translating observations of human-carnivore conflict taken at one scale to another scale more relevant to decision-makers. However, our work also underscores the lack of consistent reporting on the context and spatiotemporal dimension of studies that impede their integration into more comprehensive studies like ours, or one's ability to investigate critically important drivers such as the availability of wild prey, which might better direct management focus.

Conclusion

Moving forward, we concur with Nyhus (2016) on the use of standardized conflict metrics, such as the total numbers of animals killed, total herd sizes each year, and the proportion of the study area that these data represent, to remove some of the uncertainty surrounding such common metrics when attempting to draw inferences across disparate studies. Such standardization will ease the process of upscaling or downscaling observations and predicting where conflict might be greatest, enabling more efficient and targeted allocation of resources for management. Nevertheless, a major limitation in this work was the quality of the data, which constrained our ability to deduce spatial and temporal dimensions of a given study. The great majority of studies failed

to report either spatial or temporal resolution, eliminating ~65% of the published conflict literature from consideration herein. Spatial extent, being the study area boundary, is the simplest measure to report and was mentioned in around 90% of publications that we retained. Temporal extent was simply the duration of the study, which was also nearly always reported. In terms of variability, the spatial extent proved less variable among geographic regions than temporal extent, with developed regions conducting longer-term research (Online Resource 3). Data deficiencies were most apparent when considering resolution. As a result, authors can make their studies more useful for future meta-analyses by explicitly stating spatiotemporal dimensions. For spatial extent authors should clearly report the area over which their observations took place, and for spatial resolution, it should be clear what the minimum mapping unit or finest level of sampling was for recording conflict metrics (e.g., if records were made at the herd level, then report size of the herd as well the spatial extent over which they roamed; if at the level of a township, state the extent of the township as well as the number and size of the herds sampled therein). For temporal dimensions, authors should report the total study duration as well as the finest sampling intervals, typically months, at which data are collected and reported across the study. With consistent reporting of conflict metrics, and effective control over scaling effects, the manageable drivers of human-carnivore conflict may then come into sharper focus.

Declarations

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