

A GLOBAL ASSESSMENT OF SCALING RELATIONSHIPS FOR CARNIVORE-HUMAN
CONFLICT AND LEOPARD (*Panthera pardus*) DENSITY

Sandy A. Slovikosky

A thesis
submitted in partial fulfillment
of the requirements for the
Master of Science Degree
State University of New York
College of Environmental Science and Forestry
Syracuse, New York
April 2023

Department of Environmental Biology

Approved by:
Jacqueline Frair, Major Professor
David Newman, Chair, Examining Committee
Stephen Teale, Department Chair
Valerie Luzadis, Dean, The Graduate School

Acknowledgments

I arrived in Syracuse in the heart of the COVID-19 pandemic in August of 2020, isolated and without any connections. Now, three years later, Syracuse has become like another home due to many wonderful people. First and foremost, I extend sincerest gratitude to my advisor, Dr. Jacqueline Frair, without whom I would never have been able to study at SUNY ESF. Dr. Frair challenges her students to reach their fullest potential, yet also cares about their personal wellbeing. Her analytical and problem-solving approach to any issue helped me navigate many hurdles throughout this research process. Likewise, I am indebted to Dr. Lisanne Petracca, who was my initial link to the Frair lab and without whom I might never have joined this research group. Dr. Petracca is not only brilliant in wildlife research, lending her expertise in quantitative and spatial analyses, but is also an understanding individual who has an encouraging word whenever needed. Moreover, special thanks go to Dr. Petracca for spending an entire summer compiling the initial database of my first chapter. Finally, I thank my third committee member, Dr. Luke Hunter. His expertise in wild cats, yet humble disposition while conducting groundbreaking research, is astounding and serves as a role model for me. I am genuinely honored to have had the privilege of collaborating with someone so accomplished yet cordial.

In addition to my committee, I owe tremendous gratitude to my labmate and dear Peruvian sister, Daisy de Fátima Sánchez Mosqueda, who has been by my side through countless challenges since we started together in the fall of 2020. She has not only cared for my wellbeing in practical ways but also keeps my gaze fixed on what is most important in life. Thank you as well to labmates Stephanie Cunningham, Georgianna Silveira, Melanie Berger, and Camilo Calderón Acevedo, Frair lab affiliates Dr. Joseph Hinton and David Kramer, Dr. Eliezer Gurarie's lab, and many other faculty and students of SUNY ESF for their camaraderie

throughout this long journey. Moreover, Dr. Ophélie Couriot, Stephanie Cunningham, and Dr. Gurarie gave of their time to help me with coding and analysis issues, for which I am sincerely grateful. Lastly, special thanks go to Jessica Proctor, whose meticulous efforts in compiling the database for my second chapter saved me hours of work. Thank you very much as well to Avery Baron, and Celine Brad, for assisting with compiling the database.

There are many friends, including at SUNY ESF, Syracuse University, and outside New York State, who never failed to encourage me when I most needed it. While it is not possible to list them all here, I wish specifically to mention the staff, interns, and many students of Baptist Campus Ministry and Christian Outreach at Syracuse University, who have provided unwavering support every day and whose love is sincere. Of mention are Baptist Chaplain Devon Bartholomew, his wife Katherine, and their family, whose commitment to their students is nothing short of extraordinary. Moreover, campus ministers Anthony and Alison Rosa always provided help in any form when needed.

This entire journey would not have happened without my parents, Gary and Sonja Slovikosky, and my brother, David Slovikosky. I am blessed with the most incredible family, both immediate and extended, and to say that I would not have made it this far without them is an understatement for many reasons. I love you all! Thank you for the life you have given me.

Lastly, above all, I thank my God and Savior, Jesus Christ. Lord, thank you for placing these individuals in my life, for opening the door for me to obtain my MS degree at SUNY ESF, and for giving me a passion for carnivores and conservation. All the glory is yours, and I dedicate this thesis to you.

Epigraph

The wolf will live with the lamb,
The leopard will lie down with the goat,
The calf and the lion and the yearling together;
And a little child will lead them.
The cow will feed with the bear,
Their young will lie down together,
And the lion will eat straw like the ox.
The infant will play near the cobra's den,
And the young child will put its hand into the viper's nest.
They will neither harm nor destroy
On all my holy mountain,
For the earth will be filled with the knowledge of the LORD
As the waters cover the sea.

Isaiah 11:6 – 9, Holy Bible: New International Version (2011)

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	viii
LIST OF APPENDICES.....	ix
ABSTRACT.....	x
INTRODUCTION	1
CHAPTER 1: Scaling issues in the study of livestock depredation by carnivores.....	3
ABSTRACT.....	3
INTRODUCTION	4
METHODS	7
RESULTS	11
DISCUSSION	13
LITERATURE CITED	27
CHAPTER 2: Spatially explicit estimates of global population potential for leopard (<i>Panthera pardus</i>)	37
ABSTRACT.....	37
INTRODUCTION	38
METHODS	40
RESULTS	45
DISCUSSION	46

LITERATURE CITED	61
CONCLUSIONS.....	72
APPENDICES	74
RESUME	90

LIST OF TABLES

TABLES: CHAPTER 1	20
Table 1.1. 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)	20
Table 1.2. Parameter estimates (β) with standard errors (SE) for the most parsimonious models predicting the three metrics of conflict (percent annual loss [%loss], number of animals killed [#kills], and number of attack incidents [#attacks]).....	22
TABLES: CHAPTER 2	54
Table 2.1. AIC support for candidate models predicting log(number of leopards/100 km ²), model definitions given in Appendix 2.3.....	54
Table 2.2. Final model predicting log(density) for leopard range-wide	56
Table 2.3. Predicted population size for leopard by country	57

LIST OF FIGURES

FIGURES: CHAPTER 1.....	23
Figure 1.1. Global distribution of studies assessing livestock depredation by carnivores from a literature review of 213 peer-reviewed articles	23
Figure 1.2. Predicted relationships between spatial extent and %loss, log(#kills), and log(#attacks) from the single top models.....	24
Figure 1.3. Predicted relationships between temporal extent and %loss, log(#kills), and log(#attacks) from the single top models.....	25
Figure 1.4. Predicted relationship between the three metrics of conflict and temporal resolution from the single top models after controlling for human density and carnivore body mass.....	26
FIGURES: CHAPTER 2.....	58
Figure 2.1. Published leopard density estimates obtained using non-spatial capture-mark-recapture with a buffer of half the mean maximum (HMMDM) distance moved (x-axis) versus spatial capture-mark-recapture (y-axis; N=17, $R^2 = 0.69$).....	58
Figure 2.2. Predicted relationship from my top model between log(leopard density) (individuals/100 km ²) and temperature (A) and GPP (B).....	59
Figure 2.3. Within extant leopard range as defined by Jacobson et al. (2016), shown is the predicted leopard density (individuals/100 km ²) from my top model (A) as well as uncertainty expressed as the standard error in predicted leopard density (B)	60

LIST OF APPENDICES

Appendix 1.1a. Components of spatial and temporal extent models.....	74
Appendix 1.1b. Components of spatial and temporal resolution models	75
Appendix 1.2a. AICc model selection results for %loss (total, n = 76)	76
Appendix 1.2b. AICc model selection results for log(#kills) (total, n = 111)	77
Appendix 1.2c. AICc model selection results for log(#attacks) (total, n = 62)	78
Appendix 1.3a. AICc model selection results for %loss (temporal resolution).....	79
Appendix 1.3b. AICc model selection results for log(#kills) (temporal resolution)	80
Appendix 1.3c. AICc model selection results for log(#attacks) (temporal resolution)	81
Appendix 1.4. Residual plots of single top models fit to the three metrics of conflict.....	82
Appendix 1.5a. Studies plotted according to their latitude and longitude values, and symbolized by spatial extent (km ²)	83
Appendix 1.5b. Studies plotted according to their latitude and longitude values, and symbolized by temporal extent (years)	84
Appendix 2.1. Description of land cover classes as derived from MODIS MCD12Q1 and collapsed classes used for predicting leopard density.....	85
Appendix 2.2. Spatial data sources used to derive environmental variables for the leopard density models.....	86
Appendix 2.3. Plausible candidate models for predicting log(density) of leopard (<i>Panthera pardus</i>)	88

Abstract

S.A. Slovikosky. A Global Assessment of Scaling Relationships for Carnivore-Human Conflict and Leopard (*Panthera pardus*) Density, 104 pages, 5 tables, 7 figures, 2023. Landscape Ecology style guide used.

Synthesizing information across disparate studies remains challenging in part due to scaling issues, a concept requiring greater consideration with respect to observations of human-carnivore conflict and range-wide predictions of species status. I used published records to examine: 1) spatiotemporal scaling in livestock depredation metrics, and 2) global drivers of potential leopard (*Panthera pardus*) abundance. Generally, the apparent magnitude of livestock depredation increased with spatial and temporal extent, whereas predicted leopard density decreased with spatial extent. Temperature, primary productivity, and human impacts, measured over 1- to 20-km² spatial extents, explained 38% of the observed variation in leopard density globally after accounting for study design effects. This work provides the first spatially explicit map of potential leopard abundance from southern Africa to far-eastern Russia, sheds light on scaling relationships for carnivore conflict metrics, and discusses additional work needed to provide the most reliable information to guide conservation actions for large carnivores worldwide.

Key Words: carnivore-human conflict, density, leopard, livestock depredation, scale

S.A. Slovikosky

Candidate for the degree of Master of Science, April 2023

Jacqueline Frair, Ph.D.

Department of Environmental Biology

State University of New York College of Environmental Science and Forestry,

Syracuse, New York

INTRODUCTION

Of the many terrestrial species of conservation concern, few have received as much research attention as large carnivores, namely felids, canids, hyaenids, and ursids (Lozano et al. 2019; Ugarte et al. 2019). Given their charismatic appeal and proclivity to engage in conflict with people, many studies have focused on population status and threats to species persistence (Loveridge et al. 2010, 2022b; Jędrzejewski et al. 2018). Of focus across much of this research are local environmental drivers that influence carnivore abundances and their interactions with human activities (Gastineau et al. 2019; Wilkinson et al. 2020; Loveridge et al. 2022b).

Recognition of the importance of scale when assessing the influence of environmental and anthropogenic drivers of change for wildlife is growing (Nyhus 2016). Associations among variables may vary unpredictably with the scale of observation (Miller et al. 2015; Wells et al. 2019), affecting predictions and muddying cross-study comparisons (Miller et al. 2004; Newman et al. 2019). Although much effort has been expended on issues pertaining to large carnivore conservation, more clarity is needed to understand 1) whether human-carnivore conflict observations exhibit non-linear trends across space and time, and 2) the appropriate scales for modeling global drivers of carnivore density. Greater insight into scaling issues is needed to draw the most robust conclusions from cross-study comparisons (Dixon Hamil et al. 2016). In this thesis, I present two original data chapters, each as a publishable unit. First, based on 213 published studies, I assessed how the spatial and temporal scale of observation affected metrics of human-carnivore conflict, namely the total number of kills, attack incidents, and percent annual loss of stock. These are three metrics derivable from readily provided information that enable cross-study comparison for carnivore conflict. Next, after controlling for study design effects (including spatial scale), I used 136 published estimates to model global drivers of

leopard (*Panthera pardus*) density. I identified optimal spatial scales and non-linear relationships to attempt to predict global population size, recognizing that my ecologically-based carrying capacity estimate may not reflect actual populations on the ground but instead their potential. Each chapter meets the formatting guidelines for the journal *Landscape Ecology*.

CHAPTER 1: Scaling issues in the study of livestock depredation by carnivores

ABSTRACT

The magnitude and socioecological drivers of livestock depredation by large carnivores have been well-studied across the world. However, very few studies have assessed how observations of depredation might vary with spatiotemporal scale. Uncovering scaling relationships may allow for more accurate aggregation of observations collected at fine spatial scales, and across diverse temporal extents and resolutions, to better inform development of effective policies and management actions. Herein, I extracted data from published studies to derive conflict metrics (number of animals killed, number of attack incidents, and percent annual loss) and the spatiotemporal extent and resolution of the study. Regressions indicated positive relationships between outright numbers of attacks or animals killed and spatial and temporal extent, with a negative relationship observed for percent annual loss of stock and increasing extent. Scaling variables also interacted with other key factors known to influence human-carnivore conflict across the diverse socioecological systems reported. Data on resolution (space or time) were too sparse to draw conclusions. In fact, reporting on the spatiotemporal dimensions of a study was generally lacking. To better elucidate and control for scaling issues going forward, authors should take care to better report the spatiotemporal dimensions of their observations. With an enhanced understanding of scaling relationships in human-carnivore conflict metrics, future work may better elucidate and manage important drivers of conflict.

INTRODUCTION

Human-wildlife conflict, defined as adverse interactions between people and wildlife (Nyhus 2016), presents one of the most pressing issues facing large mammal conservation today. Large carnivores pose a safety risk to humans (Packer et al. 2005, 2019) and depredate livestock, which decreases quality of life for people. Human intolerance then becomes a threat to carnivores due to retaliatory killing (Inskip and Zimmermann 2009; Barua et al. 2013), with felids and canids considered the greatest overall offenders (Ugarte et al. 2019). Past research of human-carnivore conflict evaluation has focused on where and when conflict occurs (Inskip and Zimmermann 2009; Barua et al. 2013), 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). Many authors have pointed to the glaring absence of attention to potential scaling issues when attempting to draw inference on carnivore conflict across disparate studies (Nyhus 2016; Montgomery et al. 2018). Yet, despite a proliferation of several hundred publications on human-carnivore conflict since the 1990s (Ugarte et al. 2019; Khorozyan and Waltert 2021), potential scaling relationships remain unresolved.

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). Yet, relationships between reported rates of livestock depredation and spatiotemporal scale have not been well considered (Nyhus 2016). Uncovering the relationship between scale and human-carnivore conflict metrics may allow for better

aggregation of observations collected at fine spatial scales, and across diverse temporal extents and resolutions, to better inform effective policies and targeted management actions typically undertaken at larger spatiotemporal scales (Dixon Hamil et al. 2016). Without consideration of scale, inferences regarding conflict hotspots, magnitude, and mitigation effectiveness may well be muddied, interfering with effective conservation action. The outcomes of every natural phenomenon, including 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. 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).

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). Scale can be specifically decomposed into extent and resolution; extent being 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. 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).

While the relationship between scaling dimensions and human-carnivore conflict metrics has been assessed for single species or specific regions, such as brown bear in the French Pyrenees (Gastineau et al. 2019) or within the Yellowstone Ecosystem (Wells et al. 2019), it is unknown how robust those scaling relations 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, making prediction 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 years 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, I explicitly investigate how common measures of conflict, as reported in the published literature, vary globally with increasing spatial and temporal scale. To achieve this, I conducted a literature review of existing livestock depredation data from carnivores worldwide, restricting my search to felids, canids, ursids, and mustelids. From this body of literature, I extracted conflict metrics and recorded or inferred the spatiotemporal scale of observation. Ultimately, I regressed these metrics against spatial or temporal extent and resolution while controlling for human population density and body mass of the largest carnivore involved, given evidence that these variables are positively correlated with conflict (Woodroffe 2000; Ugarte et al. 2019).

METHODS

I searched Web of Science, from 1985 through January 2022, for peer-reviewed papers reporting livestock loss to carnivores. 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. I 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, yielding a total of 888 papers. I further 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 are 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). I included all papers that provided the necessary data to calculate these metrics when they were not directly reported. 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, I noted the spatial and temporal extents and resolutions at which data were collected. *Spatial extent* was defined as the total study area in km², while *resolution* (km²) 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.

My initial intent was to have two metrics (%loss and #kills), however because many studies reported only the number of attack incidents (#attacks) as opposed to raw totals of animals killed, I categorized these metrics separately. Nonetheless, I did not expect there to be inherent differences in scaling relationships between #kills and #attacks, given that #attacks is equivalent to a minimum number of total animals killed. I 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 taken (Stahl et al. 2001; Rosas-Rosas et al. 2008). Moreover, I predicted that while %loss would not change within the temporal dimension (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 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). Also, higher human densities could increase conflict because of greater interactions between carnivores and livestock (Mukeka et al. 2019) while larger-bodied predators might kill more livestock than smaller species (Ugarte et al. 2019) with their differing patterns of space use affecting scaling relationships across space and time.

I used multi-variable regression models to explore how depredation observations might vary by spatiotemporal extent 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, I extracted human population density (people/km²) 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, I 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*]). I 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, I included a random effect of continent to account for global ecological and socioeconomic differences in systems of human-wildlife interactions (Lozano et al. 2019).

The most informative set of covariates was identified using Akaike’s Information Criterion (AIC; Akaike 1987), with model selection uncertainty identified where $\Delta AIC_c < 2$. All models included carnivore body size (categorical) and human density (continuous) to control for their effects, including the null model (Appendices 1.1a & 1.1b). Candidate models individually included spatial extent, temporal extent, spatial resolution, and temporal resolution, as well as combinations of both spatial and temporal extent (with and without an interaction) within the same models. I was unable to combine spatial and temporal resolution within a single model due

to data limitations. Models further compared spatiotemporal covariates as either linear (x) or non-linear terms ($x+x^2$) 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.

RESULTS

From 606 published articles meeting my search criteria, I was able to sufficiently infer data on spatiotemporal scale and conflict metrics from 213 (35%). These represented five continents involving 17 carnivore species (Figure 1.1). Half of studies across all three conflict metrics involved carnivores over 100 kg, whereas a third focused on species less than 50 kg. Studies on %loss and #kills were most common in Asia (35% and 41%, respectively), whereas #attacks was mostly reported in North America (35%). The continental variable did not explain any variation in the models.

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 1.1). The top models for #attacks and #kills each included temporal extent, while the top model for %loss included both spatial and temporal extent (Table 1.1). For %loss the top model (including an interaction between spatial and temporal extent) carried 60% of the AICc weight, while a more complex model with additional interactions between spatial extent and the two control variables was also a competitor (Appendix 1.2a). Partial slopes indicated that %loss decreased with increasing spatial (Figure 1.2) and temporal (Figure 1.3) extent, with the slope for spatial extent being slightly ameliorated by increasing temporal extent.

While scaling variables were important in terms of AIC, I was unable to estimate statistically significant effects for any variables.

For #kills the single top model included human density, temporal extent, and an interaction between temporal extent and carnivore body mass (Table 1.1, Appendix 1.2b). Log(#kills) was greatest for species having body mass in the 50 – 100 kg range, being significantly greater than the largest body mass category (Table 1.2). Log(#kills) increased with greater temporal extent, with the steepest slope observed for mid-sized carnivores (Figure 1.3).

Of four competing models for #attacks, two accounted for 50% of the weight (Appendix 1.2c), and these included an interaction between temporal extent and human density or quadratic effects of spatial extent and human density. In the top model, log(#attacks) increased with increasing temporal extent, notably so in areas of higher human population density (Figure 1.3). The competing model ($\Delta AICc = 0.1$ compared to the top model) indicated a concave relationship between spatial extent and log(#attacks) (Figure 1.2), an effect that was not statistically significant. The other two competing models included either a quadratic effect of temporal extent or an interaction between spatial and temporal extent. The only statistically significant effect was temporal extent and its interaction with human density in the top model (Table 1.1). This indicates that more attack incidents occur across longer time periods at higher versus lower human densities.

In considering the effects of spatial resolution versus extent, I became data limited with only 16 or 17 data points per conflict metric. Thus, I was unable to run a separate model selection exercise for spatial resolution. Data were also sparser for temporal resolution, albeit less so ranging from 37-77 data points per conflict metric. Model selection for temporal resolution indicated a generally increasing trend between temporal resolution and all three

conflict metrics (Figure 1.4, Appendix 1.3a), with temporal resolution being retained in the top models for %loss and log(#attacks; Appendix 1.3c) although none of these effects proved statistically significant given $\alpha = 0.05$. Covariates affecting log(#kills) proved the most ambiguous with all models containing spatial or temporal covariates falling within 2 AICc units of each other, and all of them being better than the null model by more than 2 units of AICc (Appendix 1.3b). Overall, this model selection exercise corroborated the previous effort, indicating that spatial and temporal extent are important considerations when comparing conflict metrics across studies even though the relationships remain noisy.

Ultimately, residuals were normally distributed across the top models for all metrics, indicating appropriate model fit (Appendix 1.4).

DISCUSSION

Ecologists have long demonstrated how ecological patterns and processes can change over space and time, and that the window through which we record 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 my knowledge this is the first attempt to comprehensively map out globally-relevant scaling relationships. Using three common metrics depicting severity of conflict (percent loss of stock, number of animals killed, and number of attack incidents), I 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. And 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 \times temporal extent) or in combination with carnivore body size or human population density. Given highly noisy relationships, stemming in part from the inclusion of multiple livestock and predator types in the same model (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 with expectations, and have implications for gaining inference on hotspots of conflict as well as the major drivers of human-carnivore conflict.

The positive relationship observed between spatiotemporal extent and number of observed events (attack incidents or animals killed) was expected 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 increasing landscape heterogeneity with further increases in scale, such as country-level differences in biomes, human infrastructure and population size, carnivore species, number of livestock, and patchiness of livestock operations (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 (a given 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, it is unexpected

that %loss should decrease with longer time periods unless differences exist across studies in husbandry or the ecological state, such as in predator richness or wild prey abundance (Guerisoli et al. 2017; Suryawanshi et al. 2017; Chaka et al. 2021). The negative trend I observed might also be associated with my 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).

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). The lack of proper specification of resolution in most studies stymied my 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 me from exploring that to any great detail.

I 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 (Ogada et al. 2003; Graham et al. 2005; Weise et al. 2018). 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 (Rostro-García et al. 2016; Fowler et al. 2019; Mukeka et al. 2019).

I further attempted to control for predator body size by considering the largest species involved (as reported by authors) given that some studies pool livestock killed across all predator species. The largest carnivore however 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 are the primary depredators (Kissui et al. 2019). The same holds true in Nepal, where snow leopards kill more yak and horses than the larger brown bear (Chetri et al. 2019). Within Bhutan, leopards 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.

Despite my robust model selection exercise, and the detection of some statistically significant relationships, wide variation in my results especially at broader scales warrants further research on drivers of the unexplained variation. Specifically, husbandry 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 in open areas to a regional level would underestimate the magnitude if other villages were more enclosed in dense habitat, 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 (Dixon Hamil 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 (Dixon Hamil et al. 2016). I used continent as a random effect, though this variable did not account for any of the variation in the models across my metrics, suggesting that finer-scale factors like countries or biomes might account for additional heterogeneity. Such an analysis however would warrant larger sample sizes across each level of the random effect than I was able to achieve herein.

My findings suggest 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 (Dixon Hamil 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 power laws, clarify patterns, and elucidate which drivers are relevant to predicting conflict regardless of the spatiotemporal scale of data collection (Wu 2004).

Moving forward, I 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. Moreover, a major limitation in this work was the quality of the data, which constrained my 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 I 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 (Appendices 1.5a & 1.5b). 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 free 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.

TABLES: CHAPTER 1

Table 1.1. 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). 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 Δ AIC values for each model, with models contributing to model selection uncertainty indicated in **bold**.

Model description	Main effects				Interactions					K	Δ AIC		
	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 x 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 x HD	x		x	x		x				7	5.8	16.2	9.5
Spatial nonlinear	x, x ²		x	x						7	7.2	13.9	4.2
Full nonlinear	x, x ²	x, x ²	x, x ²	x	x	x	x			14	7.8	14.0	-
Spatial x CM	x		x	x			x			8	8.9	14.5	9.4
Spatial nonlinear + HD nonlinear	x, x ²		x, x ²	x						8	9.6	14.2	0.1
Temporal linear		x	x	x						6	97.0	8.4	3.0
Temporal nonlinear		x, x ²	x	x						7	98.0	5.9	2.4
Temporal x 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, x ²	x, x ²	x		8	100.4	6.4	0.4
Null		x	x		5	102.0	13.3	5.2

Table 1.2. Parameter estimates (β) with standard errors (SE) for the most parsimonious models predicting the three metrics of conflict (percent annual loss [%loss], number of animals killed [#kills], and number of attack incidents [#attacks]). 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.

	%loss (N = 76)		#kills (N = 111)		#attacks (N = 62)	
	Estimate	Standard Error	Estimate	Standard Error	Estimate	Standard Error
Intercept	1.2781	0.2000	5.6939	0.5921	5.9665	0.2902
Human Density	-0.05716	0.1616	-0.09209	0.1485	0.2212	0.2641
Carnivore Mass (50 – 100 kg)	-0.1104	0.3238	1.6338	0.5822*	-0.2552	0.6210
Carnivore Mass (<50 kg)	-0.1065	0.3065	-0.4132	0.3514	-0.3059	0.4111
Spatial extent	-0.2321	0.1537	-	-	-	-
Temporal extent	-0.2759	0.1538	0.2106	0.1682	0.6805	0.2215*
Spatial \times Temporal	0.4395	0.3641	-	-	-	-
Carnivore Mass (50 – 100 kg) \times Temporal extent	-	-	2.2447	0.6016*	-	-
Carnivore Mass (<50 kg) \times Temporal extent	-	-	0.4869	0.4238	-	-
Human Density \times Temporal extent	-	-	-	-	0.9093	0.3732*

FIGURES: CHAPTER 1

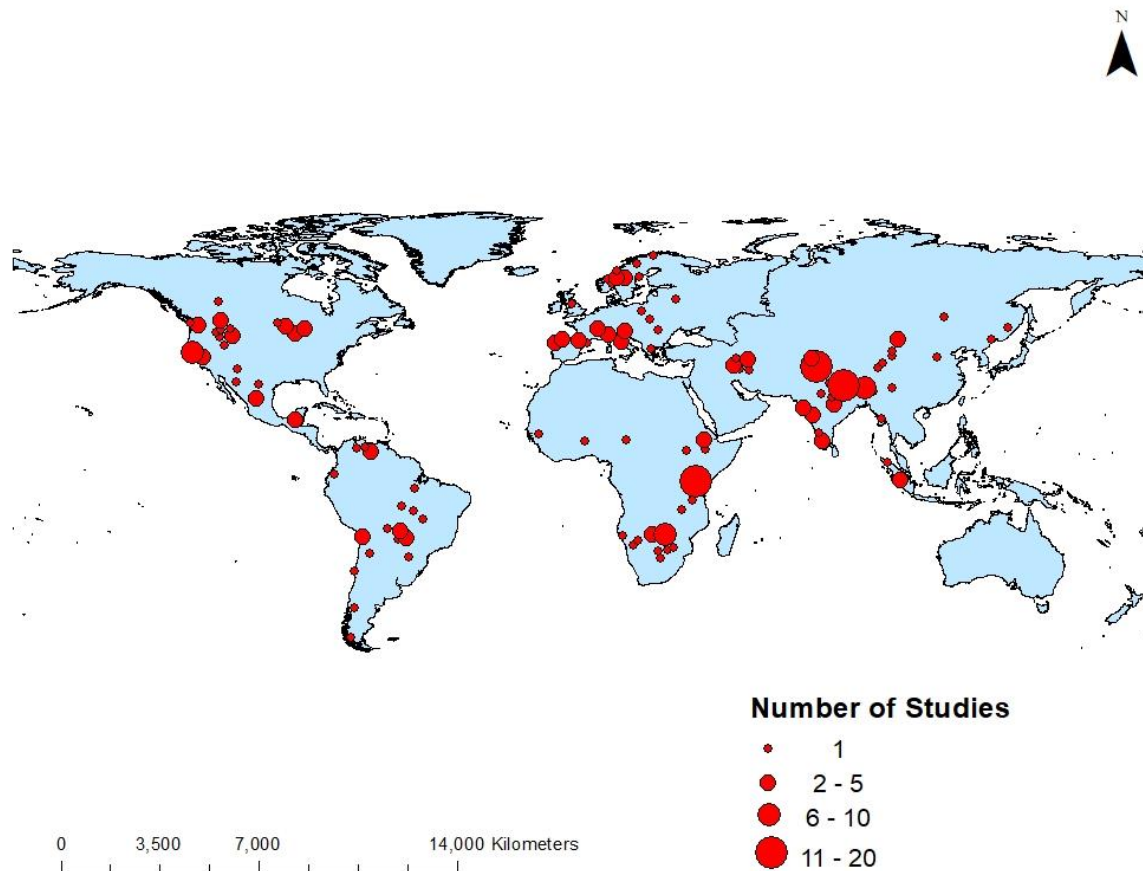


Figure 1.1. Global distribution of studies assessing livestock depredation by carnivores from a literature review of 213 peer-reviewed articles. Circle size demonstrates the local density of studies, specifically the number of studies whose location centers fell within a 100-km radius.

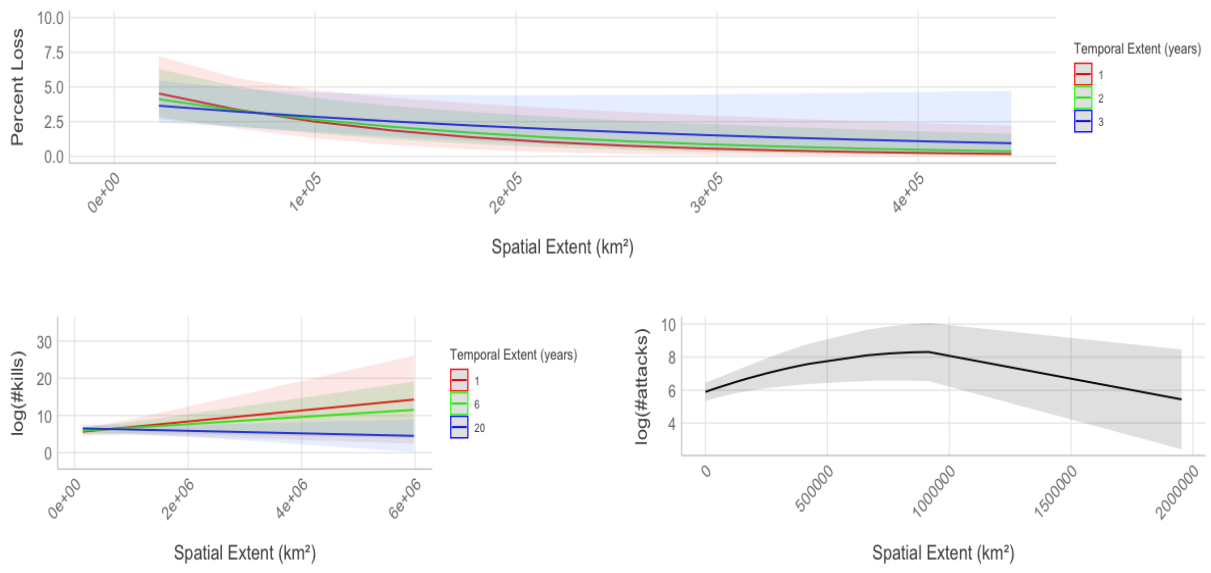


Figure 1.2. Predicted relationships between spatial extent and %loss, log(#kills), and log(#attacks) from the single top models.

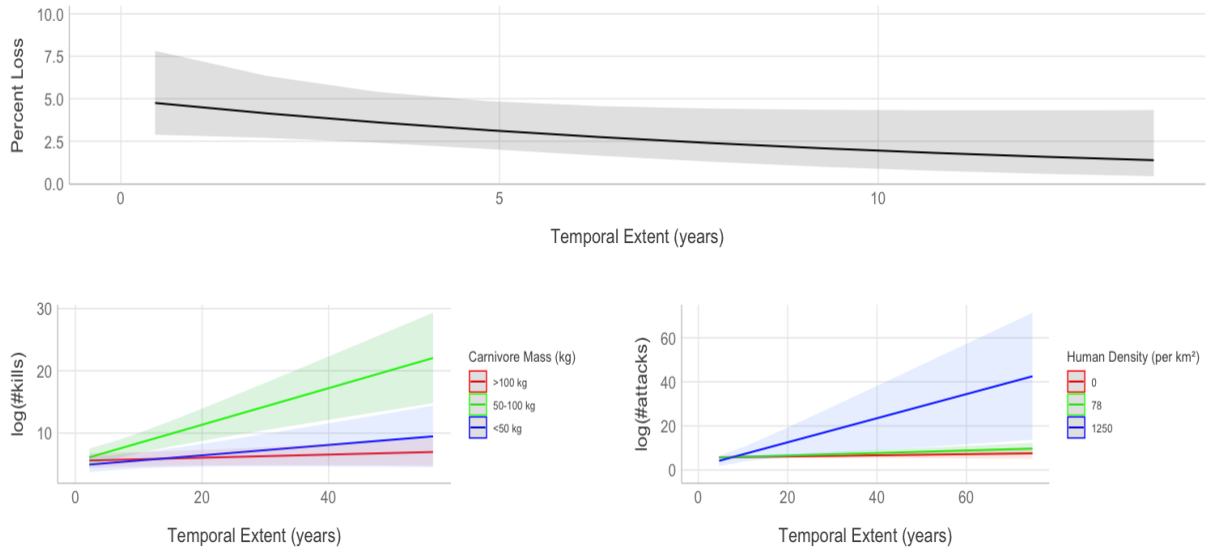


Figure 1.3. Predicted relationships between temporal extent and %loss, log(#kills), and log(#attacks) from the single top models.

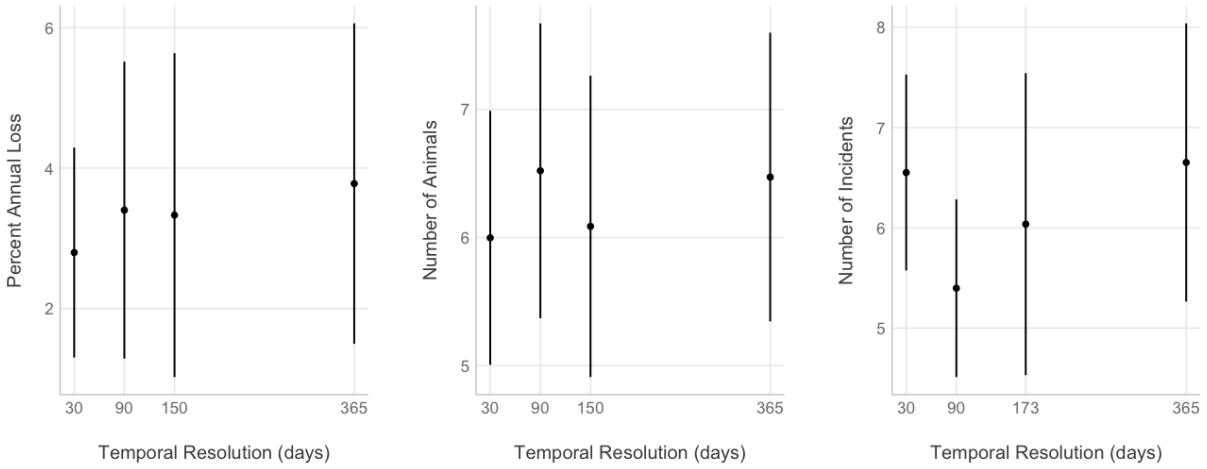


Figure 1.4. Predicted relationship between the three metrics of conflict and temporal resolution from the single top models after controlling for human density and carnivore body mass. The y-axis for number of animals and incidents is log transformed.

LITERATURE CITED

- Acharya KP, Paudel PK, Jnawali SR, et al (2017) Can forest fragmentation and configuration work as indicators of human–wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. *Ecol Indic* 80:74–83.
<https://doi.org/10.1016/j.ecolind.2017.04.037>
- Akaike H (1987) Factor analysis and AIC. *Psychometrika* 52:317–332
- Amador-Alcalá S, Naranjo EJ, Jiménez-Ferrer G (2013) Wildlife predation on livestock and poultry: Implications for predator conservation in the rainforest of south-east Mexico. *Oryx* 47:243–250. <https://doi.org/10.1017/S0030605311001359>
- Barua M, Bhagwat SA, Jadhav S (2013) The hidden dimensions of human-wildlife conflict: health impacts, opportunity and transaction costs. *Biol Conserv* 157:309–316.
<https://doi.org/10.1016/j.biocon.2012.07.014>
- Baruch-Mordo S, Breck SW, Wilson KR, Theobald DM (2008) Spatiotemporal distribution of black bear–human conflicts in Colorado, USA. *J Wildl Manage* 72:1853–1862.
<https://doi.org/10.2193/2007-442>
- Breiman L, Friedman JH (1997) Predicting multivariate responses in multiple linear regression. *J R Stat Soc Ser B* 59:3–54
- Broekhuis F, Cushman SA, Elliot NB (2017) Identification of human–carnivore conflict hotspots to prioritize mitigation efforts. *Ecol Evol* 7:10630–10639. <https://doi.org/10.1002/ece3.3565>
- Buchholtz EK, Stronza A, Songhurst A, et al (2020) Using landscape connectivity to predict human-wildlife conflict. *Biol Conserv* 248:108677.
<https://doi.org/10.1016/j.biocon.2020.108677>
- Chaka SNM, Kissui BM, Gray S, Montgomery RA (2021) Predicting the fine-scale factors that

- correlate with multiple carnivore depredation of livestock in their enclosures. *Afr J Ecol* 59:74–87. <https://doi.org/10.1111/aje.12789>
- Chetri M, Odden M, Devineau O, Wegge P (2019) Patterns of livestock depredation by snow leopards and other large carnivores in the Central Himalayas, Nepal. *Glob Ecol Conserv* 17:e00536. <https://doi.org/10.1016/j.gecco.2019.e00536>
- Conner MM, Jaeger MM, Weller TJ, McCullough DR (1998) Effect of coyote removal on sheep depredation in northern California. *J Wildl Manage* 62:690–699. <https://doi.org/10.2307/3802345>
- Dickman AJ (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Anim Conserv* 13:458–466. <https://doi.org/10.1111/j.1469-1795.2010.00368.x>
- Dickman AJ, Macdonald EA, Macdonald DW (2011) A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. *Proc Natl Acad Sci U S A* 108:13937–13944. <https://doi.org/10.1073/pnas.1012972108>
- Dixon Hamil KA, Iannone B V., Huang WK, et al (2016) Cross-scale contradictions in ecological relationships. *Landsc Ecol* 31:7–18. <https://doi.org/10.1007/s10980-015-0288-z>
- Dumbrell AJ, Clark EJ, Frost GA, et al (2008) Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. *J Appl Ecol* 45:1531–1539. <https://doi.org/10.1111/j.1365-2664.2008.01533.x>
- Eklund A, López-Bao JV, Tourani M, et al (2017) Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Sci Rep* 7:1–9. <https://doi.org/10.1038/s41598-017-02323-w>
- Fauchald P, Erikstad KE, Skarsfjord H (2000) Scale-dependent predator-prey interactions: the

- hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783.
[https://doi.org/10.1890/0012-9658\(2000\)081\[0773:SDPPIT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0773:SDPPIT]2.0.CO;2)
- Fowler NL, Belant JL, Beyer DE (2019) Non-linear relationships between human activities and wolf-livestock depredations. *Biol Conserv* 236:385–392.
<https://doi.org/10.1016/j.biocon.2019.05.048>
- Frair JL, Merrill EH, Visscher DR, et al (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc Ecol* 20:273–287.
<https://doi.org/10.1007/s10980-005-2075-8>
- Gastineau A, Robert A, Sarrazin F, et al (2019) Spatiotemporal depredation hotspots of brown bears, *Ursus arctos*, on livestock in the Pyrenees, France. *Biol Conserv* 238:108210.
<https://doi.org/10.1016/j.biocon.2019.108210>
- Götttert T, Starik N (2022) Human–wildlife conflicts across landscapes-general applicability vs. case specificity. *Diversity* 14:380
- Graham K, Beckerman AP, Thirgood S (2005) Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biol Conserv* 122:159–171.
<https://doi.org/10.1016/j.biocon.2004.06.006>
- Guerisoli M de las M, Luengos Vidal E, Franchini M, et al (2017) Characterization of puma–livestock conflicts in rangelands of central Argentina. *R Soc Open Sci* 4:.
<https://doi.org/10.1098/rsos.170852>
- Hamer KC, Hill JK (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conserv Biol* 14:1435–1440. <https://doi.org/10.1046/j.1523-1739.2000.99417.x>
- Harcourt AH, Parks SA, Woodroffe R (2001) Human density as an influence on species/area

- relationships: Double jeopardy for small African reserves? *Biodivers Conserv* 10:1011–1026. <https://doi.org/10.1023/A:1016680327755>
- Inskip C, Zimmermann A (2009) Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43:18–34. <https://doi.org/10.1017/S003060530899030X>
- Jones KE, Bielby J, Cardillo M, et al (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648–2648. <https://doi.org/10.1890/08-1494.1>
- Kaartinen S, Luoto M, Kojola I (2009) Carnivore-livestock conflicts: Determinants of wolf (*Canis lupus*) depredation on sheep farms in Finland. *Biodivers Conserv* 18:3503–3517. <https://doi.org/10.1007/s10531-009-9657-8>
- Kaczensky P (1999) Large carnivore depredation on livestock in Europe. *Ursus* 11:59–71
- Kansky R, Knight AT (2014) Key factors driving attitudes towards large mammals in conflict with humans. *Biol Conserv* 179:93–105. <https://doi.org/10.1016/j.biocon.2014.09.008>
- Khorozyan I, Waltert M (2021) A global view on evidence-based effectiveness of interventions used to protect livestock from wild cats. *Conserv Sci Pract* 3:1–14. <https://doi.org/10.1111/csp2.317>
- Kissui BM, Kiffner C, König HJ, Montgomery RA (2019) Patterns of livestock depredation and cost-effectiveness of fortified livestock enclosures in northern Tanzania. *Ecol Evol* 9:11420–11433. <https://doi.org/10.1002/ece3.5644>
- Kotliar NB, Wiens JA (1990) Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity. *Oikos* 59:253–260
- Kuiper T, Loveridge AJ, Macdonald DW (2022) Robust mapping of human–wildlife conflict: controlling for livestock distribution in carnivore depredation models. *Anim Conserv*

- 25:195–207. <https://doi.org/10.1111/acv.12730>
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
<https://doi.org/10.2307/1941447>
- Loucks OL (1970) Evolution of diversity, efficiency, and community stability. *Integr Comp Biol* 10:17–25. <https://doi.org/10.1093/icb/10.1.17>
- Lozano J, Olszańska A, Morales-Reyes Z, et al (2019) Human-carnivore relations: a systematic review. *Biol Conserv* 237:480–492. <https://doi.org/10.1016/j.biocon.2019.07.002>
- Madden F (2004) Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Hum Dimens Wildl* 9:247–257.
<https://doi.org/10.1080/10871200490505675>
- Mayor SJ, Schaefer JA (2005) The many faces of population density. *Oecologia* 145:276–281.
<https://doi.org/10.1007/s00442-005-0114-4>
- Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP (2009) Habitat selection at multiple scales. *Écoscience* 16:238–247. <https://doi.org/10.2980/16-2-3238>
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* 5:52–57. [https://doi.org/10.1016/0169-5347\(90\)90048-I](https://doi.org/10.1016/0169-5347(90)90048-I)
- Miller JRB (2015) Mapping attack hotspots to mitigate human–carnivore conflict: approaches and applications of spatial predation risk modeling. *Biodivers Conserv* 24:2887–2911.
<https://doi.org/10.1007/s10531-015-0993-6>
- Miller JRB, Jhala Y V., Jena J, Schmitz OJ (2015) Landscape-scale accessibility of livestock to tigers: Implications of spatial grain for modeling predation risk to mitigate human-carnivore conflict. *Ecol Evol* 5:1354–1367. <https://doi.org/10.1002/ece3.1440>

- Miller JRB, Stoner KJ, Cejtin MR, et al (2016) Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildl Soc Bull* 40:806–815.
<https://doi.org/10.1002/wsb.720>
- Mishra C (1997) Livestock depredation by large carnivores in the Indian trans-Himalaya: Conflict perceptions and conservation prospects. *Environ Conserv* 24:338–343.
<https://doi.org/10.1017/S0376892997000441>
- Montgomery RA, Hoffmann CF, Tans ED, Kissui B (2018) Discordant scales and the potential pitfalls for human-carnivore conflict mitigation. *Biol Conserv* 224:170–177.
<https://doi.org/10.1016/j.biocon.2018.05.018>
- Moreira-Arce D, Ugarte CS, Zorondo-Rodríguez F, Simonetti JA (2018) Management tools to reduce carnivore-livestock conflicts: current gap and future challenges. *Rangel Ecol Manag* 71:389–394. <https://doi.org/10.1016/j.rama.2018.02.005>
- Mukeka JM, Ogutu JO, Kanga E, Røskaft E (2019) Human-wildlife conflicts and their correlates in Narok County, Kenya. *Glob Ecol Conserv* 18:e00620.
<https://doi.org/10.1016/j.gecco.2019.e00620>
- Newman EA, Kennedy MC, Falk DA, McKenzie D (2019) Scaling and complexity in landscape ecology. *Front Ecol Evol* 7:293. <https://doi.org/10.3389/fevo.2019.00293>
- Nyhus PJ (2016) Human-wildlife conflict and coexistence. *Annu Rev Environ Resour* 41:143–171. <https://doi.org/10.1146/annurev-environ-110615-085634>
- Odden J, Herfindal I, Linnell JDC, Andersen R (2008) Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *J Wildl Manage* 72:276–282.
<https://doi.org/10.2193/2005-537>
- Odden J, Nilsen EB, Linnell JDC (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: The Role of Livestock Husbandry. *Conserv Biol* 17:1521–1530. <https://doi.org/10.1111/j.1523-1739.2003.00061.x>
- Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *Am Nat* 137:S29–S49. <https://doi.org/10.1086/285138>
- Packer C, Ikanda D, Kissui B, Kushnir H (2005) Lion attacks on humans in Tanzania. *Nature* 436:927. <https://doi.org/10.1038/436791a>
- Packer C, Shivakumar S, Athreya V, et al (2019) Species-specific spatiotemporal patterns of leopard, lion and tiger attacks on humans. *J Appl Ecol* 56:585–593. <https://doi.org/10.1111/1365-2664.13311>
- Patterson BD, Kasiki SM, Selempo E, Kays RW (2004) Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biol Conserv* 119:507–516. <https://doi.org/10.1016/j.biocon.2004.01.013>
- Petracca LS, Frair JL, Bastille-Rousseau G, et al (2019) The effectiveness of hazing African lions as a conflict mitigation tool: implications for carnivore management. *Ecosphere* 10:e02967. <https://doi.org/10.1002/ecs2.2967>
- Rastetter EB, King AW, Cosby BJ, et al (1992) Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecol Appl* 2:55–70
- Reed RA, Peet RK, Palmer MW, White PS (1993) Scale dependence of vegetation-environment correlations: A case study of a North Carolina piedmont woodland. *J Veg Sci* 4:329–340. <https://doi.org/10.2307/3235591>
- Rosas-Rosas OC, Bender LC, Valdez R (2008) Jaguar and Puma Predation on Cattle Calves in

- Northeastern Sonora, Mexico. *Rangel Ecol Manag* 61:554–560
- Rostro-García S, Tharchen L, Abade L, et al (2016) Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. *Landsc Ecol* 31:1277–1298. <https://doi.org/10.1007/s10980-015-0335-9>
- Sangay T, Vernes K (2008) Human-wildlife conflict in the Kingdom of Bhutan: Patterns of livestock predation by large mammalian carnivores. *Biol Conserv* 141:1272–1282. <https://doi.org/10.1016/j.biocon.2008.02.027>
- Schaefer JA, Messier F (1995) Scale-Dependent Correlations of Arctic Vegetation and Snow Cover. *Arct Alp Res* 27:38–43
- Sharma P, Chettri N, Uddin K, et al (2020) Mapping human–wildlife conflict hotspots in a transboundary landscape, Eastern Himalaya. *Glob Ecol Conserv* 24:e01284. <https://doi.org/10.1016/j.gecco.2020.e01284>
- Stahl P, Vandel JM, Herrenschmidt V, Migot P (2001) Predation on livestock by an expanding reintroduced lynx population: Long-term trend and spatial variability. *J Appl Ecol* 38:674–687. <https://doi.org/10.1046/j.1365-2664.2001.00625.x>
- Suryawanshi KR, Redpath SM, Bhatnagar YV, et al (2017) Impact of wild prey availability on livestock predation by snow leopards. *R Soc Open Sci* 4:. <https://doi.org/10.1098/rsos.170026>
- Thorn M, Green M, Dalerum F, et al (2012) What drives human-carnivore conflict in the North West Province of South Africa? *Biol Conserv* 150:23–32. <https://doi.org/10.1016/j.biocon.2012.02.017>
- Turner MG, Gardner RH (2015) *Landscape Ecology in Theory and Practice*, 2nd edn. Springer, New York

- Ugarte CS, Moreira-Arce D, Simonetti JA (2019) Ecological Attributes of Carnivore-Livestock Conflict. *Front. Ecol. Evol.* 7
- van Eeden LM, Crowther MS, Dickman CR, et al (2018) Managing conflict between large carnivores and livestock. *Conserv Biol* 32:26–34. <https://doi.org/10.1111/cobi.12959>
- Weise FJ, Hayward MW, Casillas Aguirre R, et al (2018) Size, shape and maintenance matter: A critical appraisal of a global carnivore conflict mitigation strategy – Livestock protection kraals in northern Botswana. *Biol Conserv* 225:88–97.
<https://doi.org/10.1016/j.biocon.2018.06.023>
- Wells SL, McNew LB, Tyers DB, et al (2019) Grizzly bear depredation on grazing allotments in the Yellowstone Ecosystem. *J Wildl Manage* 83:556–566.
<https://doi.org/10.1002/jwmg.21618>
- Wiens JA (1989) Spatial Scaling in Ecology. *Funct Ecol* 3:385–397
- Wilkinson CE, McInturff A, Miller JRB, et al (2020) An ecological framework for contextualizing carnivore–livestock conflict. *Conserv Biol* 00:1–14.
<https://doi.org/10.1111/cobi.13469>
- Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. *Anim Conserv* 3:165–173. <https://doi.org/10.1017/S136794300000086X>
- Wu J (2004) Effects of changing scale on landscape pattern analysis: Scaling relations. *Landscape Ecol* 19:125–138. <https://doi.org/10.1023/B:LAND.0000021711.40074.ae>
- Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q Rev Biol* 70:439–466
- Wu J, Luck M, Jelinski DE, Tueller PT (2000) Multiscale analysis of landscape heterogeneity: Scale variance and pattern metrics. *Geogr Inf Sci* 6:6–19.

<https://doi.org/10.1080/10824000009480529>

Wu J, Shen W, Sun W, Tueller PT (2002) Empirical patterns of the effects of changing scale on landscape metrics. *Landsc Ecol* 17:761–782. <https://doi.org/10.1023/A:1022995922992>

Zimmermann A, Johnson P, de Barros AE, et al (2021) Every case is different: cautionary insights about generalisations in human-wildlife conflict from a range-wide study of people and jaguars. *Biol Conserv* 260:109185.

<https://doi.org/10.1016/j.biocon.2021.109185>

CHAPTER 2: Spatially explicit estimates of global population potential for leopard

(Panthera pardus)

ABSTRACT

Although many studies have assessed local densities of threatened carnivore species, few have synthesized existing data into range-wide estimates based on habitat potential. Identifying where observed densities differ greatly from potential carrying capacity may better focus conservation attention. Herein, I related published leopard density estimates (N=136) to hypothesized drivers (e.g., gross primary productivity, human density) to produce a spatially explicit estimate of potential density throughout their geographic range spanning far-eastern Russia to southern Africa. I used AIC to identify the top model from 19 candidates that included anthropogenic and environmental drivers, alternative scales of analysis, linear and non-linear effects, and study design effects. Leopard density was negatively associated with human density and cropland and urban landscapes relative to open forest. By contrast, leopard density was positively related to temperature and primary productivity. The model explained 38% of variation in leopard density and estimated a potential for 355,000 leopards across their range. Although prediction certainty appeared greatest in areas predicted to house the most leopard, e.g., equatorial Africa and northern India, some of these areas also coincided with known low leopard numbers (due to human persecution) that I was unable to account for. Fine-scale variables and historical legacies of armed conflict that have depleted biodiversity need to be considered when evaluating contemporary leopard status, but my models may indicate population potential and where conservation action may prove most rewarding.

INTRODUCTION

Species around the world are threatened with extinction from a variety of factors, including habitat loss, overexploitation, and invasive species (Tilman et al. 2017). Data on species status informs conservation action (Nichols and Williams 2006), and involves two related but distinct aspects. First, patterns of species occurrence or site occupancy define species distributions. Monitoring changes in the geographic range of a species, especially contractions in range, remains fundamental to inferring species vulnerability to extinction and focusing conservation effort. Yet occurrence patterns alone are insufficient to ensure species persistence as the probability of site occupancy may remain constant despite an order of magnitude decline in overall species abundance (Ellis et al. 2014). The second piece of important information on species status is population density. Although generally positive (Holt et al. 2002), the relationship between site occupancy and species density is not always linear or clear (Gaston et al. 2000; Ellis et al. 2014). Hence, for rare and at-risk species, abundance estimates become critically important for monitoring conservation status (Gaston and Fuller 2009; Jones 2011) and establishing target recovery goals (Johnston et al. 2015; Loveridge et al. 2022a).

Globally, large mammals and notably large carnivores have suffered large-scale contractions of geographic range in addition to reductions in local abundance (Woodroffe 2000; Wolf and Ripple 2017). Considerable conservation and research effort has been extended to large carnivores, yielding an inordinately large number of published occupancy and abundance studies relative to smaller mammals (Srivathsa et al. 2022). The majority of studies have been conducted at the scale of individual protected areas, provinces, or countries to inform relatively fine-scale management for park or state authorities (Hebblewhite et al. 2011; Ellis et al. 2014; Wang et al. 2018; Havmøller et al. 2019; Gebretensae and Kebede 2022). Taken collectively, these disparate

studies may provide a means of evaluating range-wide habitat drivers of species abundance. For example, Jędrzejewski et al. (2018) extracted estimates of site occupancy and local density by jaguar (*Panthera onca*) from 117 published studies, and used those data to model range-wide jaguar distribution and density. Such range-wide estimates are useful for establishing baseline values against which future increases or declines can be compared, as well as prioritizing geographic regions in which conservation efforts may be most needed (Durant et al. 2007; Jacobson et al. 2016; Clavero et al. 2022; Loveridge et al. 2022a).

Large carnivores are sensitive to human predations (Darimont et al. 2015; Oriol-Cotterill et al. 2015), yet live within increasingly human-dominated landscapes (Fahrig 2007; Kowalczyk et al. 2015). Although animals may be able to spatially avoid conflict where the overall imprint of human activities is low-moderate (Basille et al. 2013), and within landscapes providing refuges, at some point human domination and modification of the landscape will lead to habitat loss and higher levels of human-carnivore conflict. Single studies in a local geographic region fail to capture variation in broad-scale context over which a species' resource selection patterns are driven, and thus can lead to confusion over globally relevant drivers of habitat quality for a species. Moreover, political boundaries will drive variation in human-exploitation patterns that may muddy the relationship between apparent habitat quality and animal abundance (Weber and Rabinowitz 1996; Nyhus 2016). As such, comprehensive modeling of species density across their range must focus on the most fundamental and globally relevant variables (e.g., relating to vegetation cover, prey base), consider that habitat relationships are likely to vary with scale of observation (Mayor et al. 2009) and, for widely distributed species, consider potential variation due to changes in ecological and political domains.

Following the approach used to model range-wide density for jaguar (Jędrzejewski et al. (2018), I modelled the density of leopard (*Panthera pardus*) across their range. By some estimates, leopard range has been reduced up to 75% (Jacobson et al. 2016). Leopard currently exist in fragmented and vulnerable populations throughout much of their range. Like jaguar, leopard exhibit a solitary and territorial nature that should facilitate density predictions. Yet, leopard are perhaps the most ecologically plastic species within the genus *Panthera* as they have the largest distribution of all wild cats – ranging from the Russian far-east to sub-Saharan Africa. As such, geographic context may drive patterns of leopard abundance beyond what we can account for with specific ecological covariates. Fortunately, the published literature on density estimates for leopard is large and geographically widespread (Balme et al. 2014; Jacobson et al. 2016). Moreover, Jacobson et al. (2016) used existing data to map the distribution of individual leopard (*Panthera pardus*) subspecies across their range, providing a contemporary range map. Leopard density, however, has not been comprehensively modeled so as to determine habitat carrying capacity and therefrom infer potential leopard abundance in unsampled areas (Stein et al. 2020). The results of this work will therefore help 1) determine features that influence leopard populations range-wide, 2) identify regions of potentially high carrying capacity to prioritize conservation attention, and 3) clarify where future data collection efforts should be focused based on prediction uncertainties and lack of available estimates.

METHODS

I searched for published estimates of leopard density in Web of Science, Google Scholar, and the International Union for Conservation of Nature (IUCN) Cat Specialist Group database using the following search terms: leopard AND (densit* OR number*), and *Panthera pardus* AND (densit*

OR number*). I excluded studies that did not include density estimates, such as those reporting abundances solely without providing information sufficient to derive density with certainty, in addition to those reports solely focusing on species other than the common leopard (ex. clouded leopard *Neofelis spp.* or leopard cat *Prionailurus bengalensis*). I recorded point estimates for density, upper and lower confidence bounds, and type of capture-recapture analysis employed. Two common methods were reported: non-spatial versus spatial capture-recapture. Non-spatial analyses added a buffer around the trap array, equivalent to the mean or half of mean maximum distance moved (MMDM and HMMDM, respectively) by the species of interest, to account for effective area sampled (Karanth and Nichols 1998). For papers that provided both spatial and non-spatial estimates, I retained only the spatial estimates. Moreover, where both Bayesian and maximum likelihood approaches were reported, I retained the more conservative estimate of the two (mean observed difference in density = 0.01 ± 0.68 SE, N = 21). If only non-spatial estimates were provided, I used MMDM estimates where available. HMMDM is known to generally overestimate density (Sharma et al. 2010). Thus, following Jędrzejewski et al. (2018), for those studies reporting both HMMDM and spatial density estimates I fit a line between the two enabling correction of HMMDM estimates in papers where they were solely reported. For studies that reported density estimates for multiple years, I retained the most recent estimate only.

I built a spatial database within a Geographic Information System of leopard densities based on latitude and longitude coordinates of the center of each study location, either as directly provided in the paper or deduced from study area description. At each location I extracted environmental and anthropogenic covariates presumed to influence leopard densities. Covariates included human population density (Woodroffe 2000), human footprint index (Sanderson et al.

2002), a binary variable indicating whether the study was in a protected area (PA; Rogan et al. 2022), terrain ruggedness index (TRI; Riley et al. 1999; Rather et al. 2021), categorical land cover type (Rather et al. 2021; Loveridge et al. 2022b), mean forest canopy cover, the normalized difference water index (NDWI), and mean annual temperature and precipitation. With respect to protected areas, I excluded IUCN protection level categories V and VI because these have less strict measures of protection although I kept any area classified as “national park” or “national reserve” (Jacobson et al. 2016). I also included several indices of productivity that might affect prey biomass, specifically the enhanced and normalized difference vegetation indices (EVI and NDVI; Sims et al. 2006; Pettorelli et al. 2011; Searle et al. 2021), and gross and net primary productivities (GPP and NPP). I further included a binary variable indicating whether the study was in Africa or Asia to account for broad, continental-scale differences in drivers of leopard density (Woodroffe 2000; Jacobson et al. 2016). Originally, I also included latitude and longitude to account for broad geographic trends, however as neither of these variables improved model fit, they were excluded. With respect to land cover, I reclassified the original eight classes (see Appendix 2.1 for variable descriptions) into three categories based on those having similar effect sizes in initial models: 1) open forest and herbaceous (reference level), 2) dense forest and croplands, and 3) shrubland and urban. Mean annual temperature, precipitation, human density, and human footprint were directly downloaded from the web with the remaining data obtained via Google Earth Engine (Appendix 2.2). Temporal periods of data extraction generally corresponded to mean values across the range of years represented (1998 - 2019). Raster layers were converted to the WGS 1984 World Mercator projection at a 1 km² resolution. At each record of leopard density covariates were extracted as the average value within five different buffer sizes: 1-, 5-, 10-, 15-, and 20-km radius (McGarigal et al. 2016;

Loveridge et al. 2022b). Leopards move an average distance of 1-km in six hours (McManus et al. 2021), and a 5-km buffer loosely corresponds to the minimum radius of a leopard's home range (Simcharoen et al. 2008; Stein et al. 2011). The 10- and 15-km buffers therefore fall within expected home range diameter. The 20-km buffer captures broad-scale habitat selection behavior (Rather et al. 2020). I then screened for potential correlations among variables and removed from my candidate variables pairs of variables having Pearson $r \geq 0.70$ (Dormann et al. 2013) to guard against multicollinearity. After testing correlated pairs of variables using univariate models, I removed the less informative from further consideration (thereby excluding mean forest canopy cover, NDVI, EVI, and NPP).

All candidate models included four variables to control for potential design effects. First, following Mishra et al. (2017), I included the area sampled (km^2) as either the minimum convex polygon (MCP; spatial analyses) or effective trapping area (non-spatial analyses, pertaining to the MCP plus a buffer). Second, following Noor et al. (2020), I included survey length as the number of study days (i.e., the maximum length of time during which any part of the trapping array was sampled given that splitting study areas into sections and rotating cameras throughout is a common practice). Third, following Rather et al. (2021), I included the number of camera trap sites (i.e., the number of stations as opposed to the number of individual cameras). Lastly, following Vinks et al. (2022), I included the number of trap nights as the number of individual cameras multiplied by the number of nights those cameras were operating.

Prior to fitting models, I log-transformed leopard density and centered and scaled all continuous covariates. To determine the optimal scale for each predictor variable (McGarigal et al. 2016; Loveridge et al. 2022b), I regressed $\log(\text{density})$ in turn against a given covariate expressed at each of the five scales while controlling for all other covariates (each included at the

10 km scale), compared the five resulting models using Akaike's Information Criterion (AIC), and identified the optimal scale from the model yielding the lowest AIC value. Next, I tested for non-linearity in covariate effects by comparing models including linear terms to models containing quadratic terms using AIC (Rogan et al. 2022). After determining the optimal scale and form for each covariate, I compared plausible candidate models using AIC (Appendix 2.3). Plausible candidate models included a null model (containing the four design-based covariates only), a full model (all 12 covariates plus a quadratic term for temperature and GPP in addition to the design-based covariates), subsets of covariates specific to human impacts alone versus environmental conditions without human impacts, and the global model less each covariate in turn. If there were competing models ($\Delta AIC < 2.0$), I retained covariates that appeared in each of the competitors to obtain a final model. This model was then compared against the global model using AIC to determine whether excluding given covariates substantially improved fit. Having chosen my best model, I used 5-fold cross validation and the resulting coefficient of determination (R^2) to validate model predictions using the `trainControl` function in R.

The final model was projected across the known extant range of leopard as defined by the species' IUCN Red List distribution map based on Jacobson et al. (2016). Prior to this extrapolation, data values within raster layers were truncated to match the range of values used during model fitting. Moreover, I masked predictions within three land cover classes ("barren," "snow and ice," and "water") that did not occur in my training data and are known to be avoided by leopards (Gavashelishvili and Lukarevskiy 2008). To map density predictions, I first used the focal statistics tool in ArcMap to summarize each raster layer at the optimal scale as previously identified. Each 1-km² cell was converted to a dataframe of points containing values for each covariate and then imported to R. Using the `predict` function in R, I applied the final model to the

dataframe to predict log(leopard density) with 95% confidence intervals resulting in three new dataframes (mean density, lower 95% confidence interval, and upper 95% confidence interval), which were converted to raster layers and imported to ArcGIS. These layers were exponentiated to convert back to the original density scale per 100 km². Ultimately, following Jędrzejewski et al. (2018), I resampled the landscape to a 100 km² resolution by averaging values across 1-km² cells, with the resulting grid representing local leopard abundance within each 100 km² cell. I then summed cell values to estimate regional (e.g., country-wide) and range-wide potential population sizes. Lastly, I represented prediction uncertainty based on the standard errors of predictions. All analyses were conducted within program R 4.2.2 and ArcMap 10.8.1.

RESULTS

Of the 456 estimates of leopard density that I extracted from the published and grey literature, I retained 170 independent estimates meeting my selection criteria. Two-thirds of these came from the African continent, with South Africa most represented (N = 80, 70% of the African observations). The great majority of data (78%) stemmed from either maximum likelihood (N = 65) or Bayesian (N = 68) based spatial capture-recapture approaches, while non-spatial methods comprised 22% (N = 37). Eighteen studies reported both spatial and non-spatial (HMMDM buffer) methods, which after removing one outlier based on high leverage, yielded a significant relationship ($y = 0.83 \times \text{non-spatial density} - 0.22$, $R^2 = 0.69$, $p < 0.01$; Figure 2.1) used to correct HMMDM density estimates. Given missing values for several explanatory variables, my models were fitted to 136 data points.

There were initially five competing top models (Models 2-6; Table 2.1), each of which included mean annual temperature (quadratic), GPP (quadratic), human density, NDWI, and land

cover (K=13 parameters total), indicating these to be the most influential covariates predicting leopard density range-wide. Protected areas, TRI, human footprint, precipitation, and the continental indicator variable did not consistently appear in top models, and excluding these five variables yielded a top model having AICc weight of 0.94 (Model 1; Table 2.1). Within this top model, the scale at which variables were optimally measured varied from 20-km radius for mean annual temperature and land cover, to 5-km radius for NDWI, and 1-km radius for both GPP and human density (Table 2.2). Leopard density was positively associated with NDWI, low to intermediate values of temperature and GPP (Figure 2.2), and greater amounts of open forest/herbaceous-dominated land cover. In contrast, leopard density declined with increasing human density, amounts of dense forest/cropland, and shrub/urban land cover. Of the variables included to account for design effects, only the area sampled had a statistically significant and negative effect ($p < 0.01$) on estimates of leopard density.

Based on 5-fold cross validation, this model effectively explained only 38% of variation in leopard density ($R^2 = 0.38$), indicating the lack of key local variables driving variation in leopard populations. Predictions ranged from 0-20 leopards/100 km², whereas the highest reported density observed within the training dataset was 18 leopards/100 km² in Mudumalai Tiger Reserve in India (Ramesh 2010). The model predicted the highest potential leopard densities in northern India and near equatorial Africa, the latter being an area where on-the-ground data on leopard populations is particularly sparse (Figure 2.3A). Yet prediction uncertainty was greater in areas of lower rather than higher predicted leopard density (Figure 2.3B).

DISCUSSION

Leopard are one of the most broad-ranging and ecologically adaptable carnivore species, tolerating extreme variation across their range in terms of habitat and environmental conditions, and making efforts to predict their density range-wide challenging. Models including variables related to food, cover, and water limitations explained 38% of the variation in estimates of leopard density, surprisingly similar to the 45% of variation explained by Jędrzejewski et al. (2018) for jaguar across their considerably more narrow ecological range. Importantly, one should consider the model predictions herein as potential leopard abundance based on ecological conditions rather than estimates of current leopard status. Local variables such as the legacy of armed conflict that have depleted biodiversity (Dudley et al. 2002), and current efforts to control human-leopard conflict (Balme et al. 2009), will play a large role in determining contemporary leopard status and lead to potentially major discrepancies between model predictions based on habitat potential and how many leopards occur in a region. For this reason, density predictions (Figure 2.3) may best be interpreted through the lens of relative rather than absolute abundance. In terms of relative abundance, predictions of the highest potential leopard densities in northern India and lowest densities in eastern Asia, like China and Russia, are consistent with previous findings (Kalle et al. 2011; Vitkalova et al. 2018). However, predictions of high relative abundance in places like Angola (Table 2.3) may not reflect contemporary reality. Yet, in highlighting areas where discrepancies occur between potential and realized population sizes, this work may be useful for focusing conservation attention in areas where leopards need it most.

Carnivore densities generally increase with measures of productivity such as NDWI and GPP due to a higher abundance and assimilation of prey (Woodroffe 2000; Carbone and Gittleman 2002; Valeix et al. 2010; Jędrzejewski et al. 2018), and typically decrease with higher human densities, patterns we observed here for leopard. In comparison to the reference level of

open forest and herbaceous, which reflect optimal leopard habitat in the form of savannas and associated open woodlands (Balme et al. 2007, 2019), I observed leopard densities to be lower with increased urbanization and in habitats interspersed with croplands. These latter variables reflect the human footprint and could be associated with poor habitat or persecution of large carnivores that engage in conflict with people (Constant et al. 2015; Mukeka et al. 2019). Rogan et al. (2022) found a negative association between human footprint and leopard density, whereas Loveridge et al. (2022b) documented a similar relationship with regard to snaring hotspots and risk of trophy hunting. As in this study, Loveridge et al. (2022b) also found lower leopard densities in shrubland-dominated habitats, which could reflect less tree cover and therefore a lower probability of a successful hunt (Balme et al. 2007). Further, whereas lower leopard densities in dense forest as opposed to open forest were unexpected in my study, this relationship could reflect lower catchability of prey in dense habitat and, therefore, a proclivity to disperse to habitats with higher prey accessibility (Balme et al. 2007). This conclusion is reinforced by leopard density being best predicted by open water (here reflected in NDWI) at the 5-km scale in this study, likely due to the high concentration of prey around open water sources (Valeix et al. 2010). Alternatively, lower leopard densities in dense vs. open forest could be related to the broad-scale nature of this study and diversity of ecoregions represented.

I estimated particularly high potential leopard densities in several areas where I lacked local estimates, notably near the equator within the Republic of the Congo (RC), Central African Republic (CAR), and Angola. Prediction uncertainty was generally low within these equatorial areas, probably because productivity is highest near the equator in the form of forests and woodlands (Ugbaje et al. 2017), providing optimal habitat, abundant prey, and consequently smaller leopard home ranges (Rodríguez-Recio et al. 2022). Nevertheless, central Africa also has

a history of civil unrest, with negative ramifications for large mammals (Dudley et al. 2002). Given my prediction of a high carrying capacity within the RC, CAR, and Angola, these countries represent an important potential focus for future leopard conservation, especially since they include some of the most apparently intact leopard range (Jacobson et al. 2016). Tanzania had the third highest estimate of potential leopard numbers (22,291 – 36,461 leopards; Table 2.3), a potentially achievable carrying capacity given the presence of the Serengeti National Park (Allen et al. 2020). Prior work indicated ≥ 5 -6 leopards/100 km² in Tanzania (Allen et al. 2020; Searle et al. 2021), and disparities in predicted vs. actual leopard densities used in this study were < 2 leopards/100 km². Within Asia, I predicted the highest potential densities within the heavily protected forests bordering India, Bhutan, and Nepal, an observation consistent with previous work (Harihar et al. 2011; Goldberg et al. 2015). Differences in predicted vs. actual estimates in these countries were ~ 2 to 3 leopards/100 km². Overall, I estimated Africa to have more leopards than Asia, and India to have the highest potential abundance of leopards on a country level. These results are consistent with Jacobson et al. (2016) who reported that three leopard subspecies compose 97% of extant leopard range, including the African (*P. p. pardus*) and Indian (*P. p. fusca*) subspecies.

Generally, areas where I predicted low potential densities of leopard also corresponded with higher prediction errors and, therefore, increased prediction uncertainty. Within western South Africa, Botswana, and Namibia, my lower estimates mirror previous work that documented less than 1 individual/100 km² in these regions after accounting for bias from non-spatial methods (Stein et al. 2011; Devens et al. 2018). For instance, within Namibia, leopards respond to the presence of farmlands with larger home ranges and therefore lower densities (Marker and Dickman 2005). For the Middle East, low estimates are likely caused by small,

isolated populations and lack of transboundary conservation initiatives (Zafar-ul Islam et al. 2018; Farhadinia et al. 2021). However, higher uncertainty also was observed within southwestern Africa and Middle Eastern countries, such as Iran, which could be caused by sparser data available in these regions with which to parameterize my models. Moreover, the estimates within the southwestern corner of South Africa were several orders of magnitude different from those in the northeastern part of the country, where abundant data exist, potentially inflating the standard error. Reported leopard densities vary from under 1 individual/100 km² near Cape Town (Devens et al. 2018) to over 10 individuals/100 km² in the reserves near the east coast (Balme et al. 2010). Across South Africa model predictions differed from observed densities by up to 5 leopards/100 km². Higher uncertainty likewise existed within the northeastern parts of the species' range where the low predicted carrying capacity (158 – 678) was expected given that the critically endangered Amur leopard (*P. p. orientalis*) has the lowest remaining extant range (Jacobson et al. 2016). Disparities between predicted vs. actual estimates in the northeast and Middle East were low, <1 leopard/100 km².

I estimated the global leopard population to potentially reach 355,000 individuals on average, an estimate we know to be biased high. A more accurate picture of global abundance will not be possible until additional research considers finer-scale factors influencing leopard abundance that were unavailable to this current modeling effort. Important local predictors likely include human activities (i.e., bushmeat poaching, trophy hunting, rebel activity, civil war; Dudley et al. 2002; Packer et al. 2011; Rosenblatt et al. 2016), non-lethal costs of human presence (Creel 2018), interference competition with large predators (i.e., tigers and lions; Steinmetz et al. 2013; du Preez et al. 2015; Loveridge et al. 2022b), habitat fragmentation (Crooks 2002; Swanepoel et al. 2013), spatial distribution of prey in response to seasonal shifts

(Mduma et al. 1999; Allen et al. 2020), and management to restrict human activities or improve habitat quality (Rosenblatt et al. 2016; Havmøller et al. 2019; Searle et al. 2021). Although it was not possible to include all these covariates in a range-wide comparison like this, my analysis uncovered landscape and environmental features that are broadly relevant to leopards and identifies regions of prediction uncertainty. I note that lack of data availability for the covariates I did include, specifically area sampled and number of camera trap sites, led to the exclusion of ~20% of the data available for model fitting. Thus, within future work, consideration of the aforementioned factors could shed light on the underlying causes of potential bias and uncertainty when predicting leopard density.

A few other limitations of this study bear consideration. First, nearly half my data points originated from South Africa and northern India, so I lacked sufficient representation of leopard populations and ecological conditions across their extant range. Moreover, much of the published data on leopard density occurred within protected areas (Balme et al. 2014). Although I attempted to account for protected areas within my models, this variable was excluded during AIC model selection. Indeed, leopards are highly adaptable predators that can maintain sustainable populations both within game reserves and in lands interspersed with farming areas and high levels of harvest (Chase Grey et al. 2013; Swanepoel et al. 2015). It is worth noting, though, that my definition of protected areas excluded lesser protected IUCN categories (V and VI), which might be unexpectedly intact (Leroux et al. 2010) and significantly influence carnivore abundances. Second, I pooled all leopard subspecies into a single analysis, although given their generalist nature, leopards might be differentially influenced by various habitat types depending on the continent on which they are found. For instance, in Thailand, leopards prefer mixed deciduous and dry evergreen forests (Simcharoen et al. 2008), whereas in South Africa,

leopards principally hunt in open bushvelds (Balme et al. 2007). Yet again, I incorporated an indicator variable for Africa and Asia to account for continental differences, although this variable also was excluded in model selection. Nevertheless, stark differences may even exist within a country or among similar habitat types. For example, in Tanzania, published leopard densities differed by >2 individuals/100 km² within the same mixed-use landscape based on differences in woodland habitat and levels of protection (Searle et al. 2021). Given the uneven distribution of data geographically, I did not have sufficient data across all subspecies for finer regional analysis, nor did I have the power for continental or regional interactions with environmental covariates. Lastly, the timespan of my data is worth noting as it ranges from 1998 – 2019 during which time human density and human-dominated habitat (variables that influence leopard density) have certainly changed.

My study reflects the importance of landscape-scale conservation for the leopard albeit with fine-scale considerations for management. Leopards select for landscapes at broad scales (20 – 30 km) based on environmental conditions that reflect ideal habitat and abundant prey (Rather et al. 2020), but might select for features at fine spatial or temporal scales within those landscapes to track prey or avoid human settlements (Odden et al. 2014). In addition to conserving sufficient natural herbaceous and open forest habitat at the home range scale, management should therefore also consider ways by which leopards at finer scales might traverse around human settlements located within those landscapes, such as through maintaining connectivity between adjacent resourceful habitat patches (Llaneza et al. 2018; Suraci et al. 2020). By identifying regions of potentially high leopard densities where data are lacking on contemporary leopard status, my work highlights where research attention is still needed. Focusing studies in areas like equatorial Africa can verify whether the habitat and socioeconomic

context are indeed of sufficient quality to support a large leopard population. Moreover, geographic regions with low predicted densities can clarify which subspecies need immediate conservation attention in the form of transboundary cooperation, reduction in poaching and illegal trade, and restoration of habitat connectivity. Additional work is also required in regions of high prediction uncertainty to determine fine-scale ecological or socioeconomic factors affecting that variation. This study presents a starting point for such future inquiries by identifying environmental and anthropogenic features that influence leopards range-wide, and provides baseline values of potential abundance to guide management and target recovery goals. Conservation attention should then be focused in areas where the disparity between predicted and actual densities is greatest.

TABLES: CHAPTER 2

Table 2.1. AIC support for candidate models predicting $\log(\text{number of leopards}/100 \text{ km}^2)$, model definitions given in Appendix 2.3. Shown for each model is the number of parameters estimated (K), model log-likelihood (LL), ΔAIC values, and AIC weight.

Model	K	LL	ΔAIC	AIC Weight
Global – PA, TRI, human footprint, precipitation, and continental indicator	13	-143.20	0.0	0.94
Global – PA	17	-142.40	8.8	0.01
Global – TRI	17	-142.43	8.8	0.01
Global – human footprint	17	-142.45	8.9	0.01
Global – precipitation	17	-142.54	9.1	0.01
Global – continental indicator	17	-142.77	9.5	0.01
Global	18	-142.39	11.5	0.00
Global – temperature and precipitation	15	-147.14	13.0	0.00
Global – temperature	16	-146.35	14.0	0.00
Human	11	-152.74	14.1	0.00
Global – GPP	16	-146.75	14.8	0.00
Global – quadratic temperature	17	-145.50	15.0	0.00
Global – quadratic GPP	17	-146.12	16.2	0.00
Global – quadratic terms	16	-147.90	17.1	0.00
Global – NDWI	17	-146.99	18.0	0.00
Environmental	16	-149.62	20.4	0.00
Global – human density	17	-149.43	22.7	0.00

Global – land cover	16	-154.82	31.0	0.00
Null	5	-171.68	38.1	0.00

Table 2.2. Final model predicting log(density) for leopard range-wide. Shown is the estimated coefficient value (β ; for centered and standardized variables), standard error (SE), and upper (UPR) and lower (LWR) 95% confidence interval bounds. Variables organized between environmental effects affecting density and design effects (aspects of study design for each density estimate in the data sample) that may explain sampling variance. A bolded coefficient indicates confidence intervals excluding zero.

Variable	Scale (buffer radius)	β	SE	UPR	LWR
<i>Environmental effects:</i>					
Temperature	20 km	-0.0025	-0.1235	-0.25	0.24
Temperature ²	20 km	-0.2285	0.0884	-0.40	-0.05
GPP	1 km	0.0012	0.0757	-0.15	0.15
GPP ²	1 km	-0.1544	0.0641	-0.28	-0.03
Human density	1 km	-0.2500	0.1029	-0.45	-0.05
NDWI	5 km	0.3735	0.0993	0.18	0.57
Land cover:*					
Dense forest/cropland	20 km	-0.4562	0.1491	-0.75	-0.16
Shrub/urban	20 km	-1.4290	0.3239	-2.07	-0.79
<i>Design effects:</i>					
Area sampled		-0.0002	<0.0001	-0.0002	-0.0001
Camera sites		-0.0001	0.0016	-0.0033	0.0030
Study days		-0.0008	0.0008	-0.0024	0.0009
Trap nights		<0.0001	<0.0001	<-0.0001	<0.0001

*Reference category was open forest/herbaceous (20 km)

Table 2.3. Predicted population size for leopard by country.

Country	Predicted N (95% CI)	Country	Predicted N (95% CI)
India	34,962 (24,845 – 50,119)	Somalia	789 (571 – 1,096)
Angola	30,395 (24,092 – 38,417)	Indonesia	734 (450 – 1,218)
Tanzania	28,576 (22,291 – 36,461)	Turkey	664 (431 – 1,033)
Democratic Republic of the Congo	22,244 (15,902 – 31,291)	Equatorial Guinea	656 (448 - 964)
Mozambique	19,898 (15,694 – 25,266)	Burkina Faso	608 (403 - 920)
Central African Republic	18,107 (13,831 – 23,726)	Eritrea	601 (432 - 838)
South Africa	16,197 (12,091 – 21,934)	Thailand	585 (401 - 860)
Ethiopia	15,573 (11,464 – 21,191)	Nigeria	544 (402 - 735)
Iran	15,113 (10,079 – 22,783)	Ghana	509 (362 - 717)
Congo	12,921 (9,313 – 18,001)	Benin	465 (316 - 687)
Gabon	12,127 (8,706 – 16,935)	Swaziland	454 (343 - 609)
South Sudan	11,975 (9,010 – 15,938)	Malaysia	441 (297 - 659)
Namibia	11,675 (8,315 – 16,629)	Malawi	401 (307 - 523)
Kenya	11,004 (8,156 – 15,010)	Bangladesh	336 (240 - 472)
Botswana	10,630 (7,883 – 14,462)	Russian Federation	323 (158 - 678)
Zambia	9,909 (7,910 – 12,408)	Guinea-Bissau	312 (233 - 418)
Zimbabwe	6,575 (5,237 – 8,285)	Azerbaijan	272 (178 - 421)
Nepal	6,477 (4,653 – 9,221)	Cambodia	252 (194 - 330)
Cameroon	5,652 (4,228 – 7,573)	Mali	195 (134 - 286)
Uganda	3,087 (2,377 – 4,027)	Saudi Arabia	178 (124 - 257)
Chad	2,396 (1,640 – 3,490)	Armenia	138 (85 - 225)
China	2,280 (1,242 – 4,503)	Yemen	120 (78 - 186)
Myanmar	1,831 (1,352 – 2,492)	Oman	101 (72 - 142)
Côte d'Ivoire	1,487 (1,095 – 2,020)	Rwanda	97 (76 - 125)
Guinea	1,311 (1,000 – 1,721)	Afghanistan	61 (21 - 179)
Pakistan	1,231 (796 – 1,980)	Georgia	48 (24 - 102)
Iraq	1,228 (838 – 1,805)	Djibouti	47 (31 - 70)
Bhutan	1,168 (753 – 1,861)	Lesotho	15 (11 - 22)
Senegal	1,034 (698 – 1,532)	Sierra Leone	14 (11 - 19)
Sri Lanka	1,008 (651 – 1,588)	Niger	11 (7 - 18)
Liberia	991 (746 – 1,316)	Togo	5 (3 - 7)
Sudan	931 (691 – 1,260)	Burundi	5 (4 - 6)
Turkmenistan	799 (548 – 1,170)		

FIGURES: CHAPTER 2

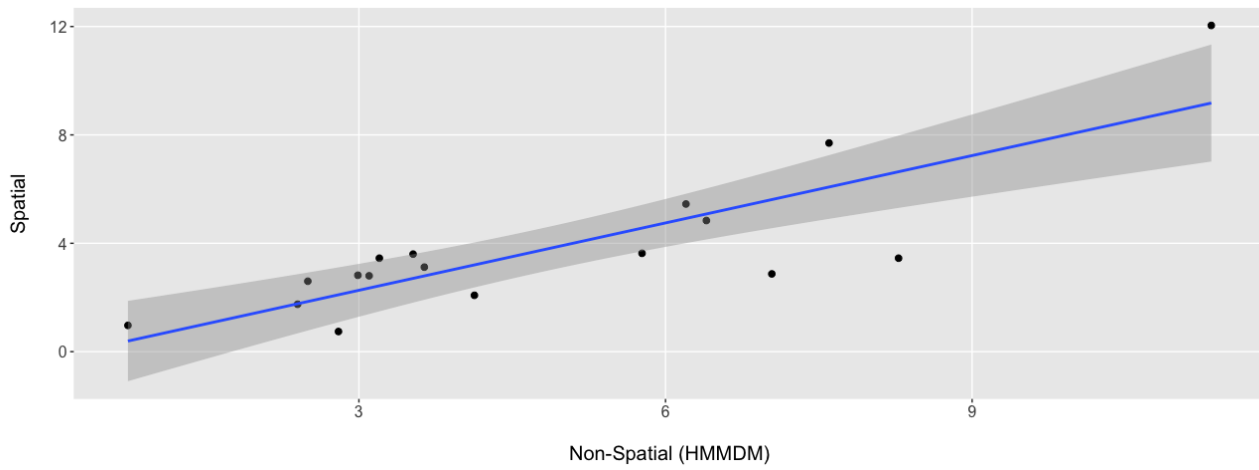


Figure 2.1. Published leopard density estimates obtained using non-spatial capture-mark-recapture with a buffer of half the mean maximum (HMMDM) distance moved (x-axis) versus spatial capture-mark-recapture (y-axis; $N=17$, $R^2 = 0.69$).

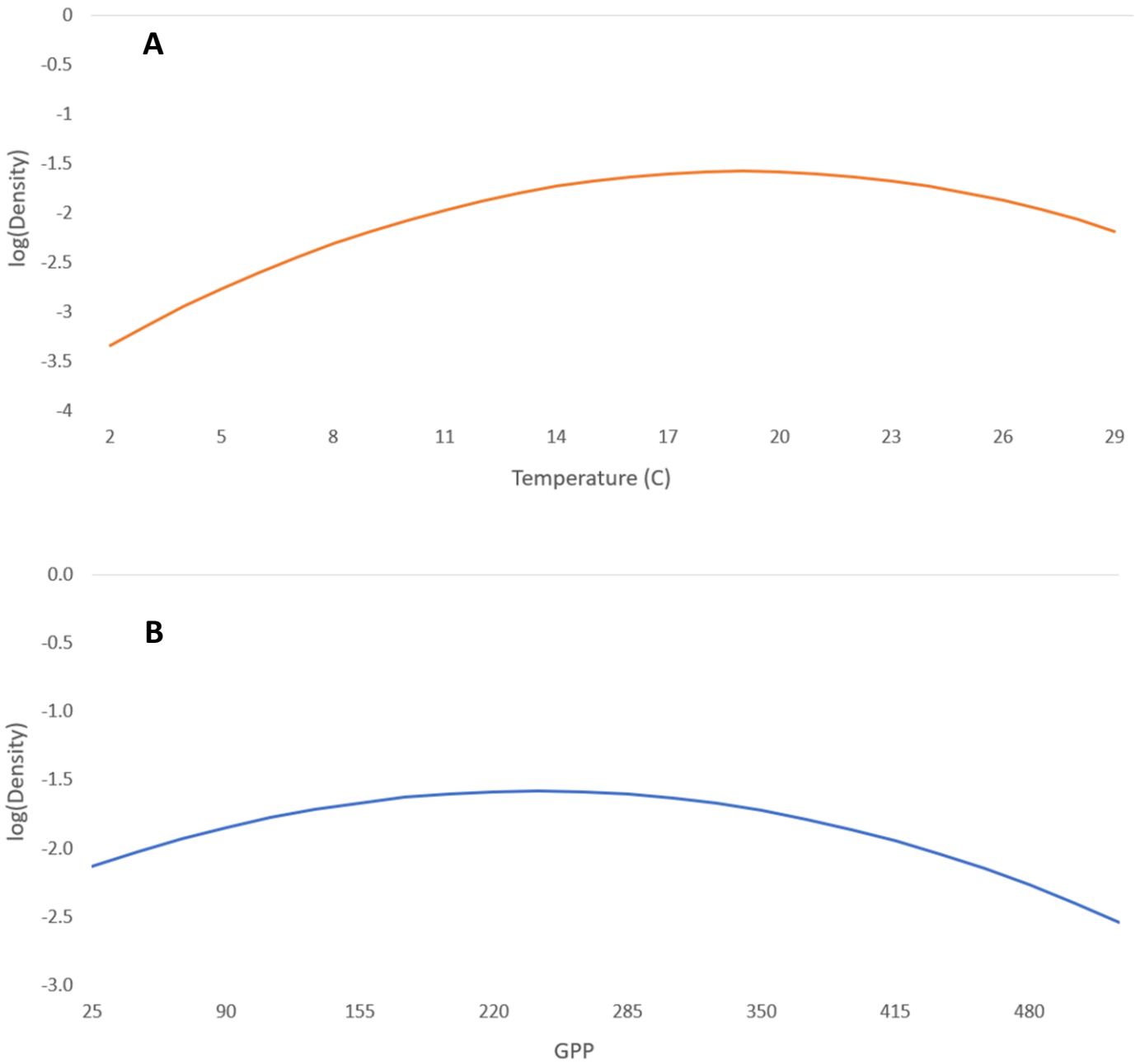


Figure 2.2. Predicted relationship from my top model between log(leopard density) (individuals/100 km²) and temperature (A) and GPP (B).

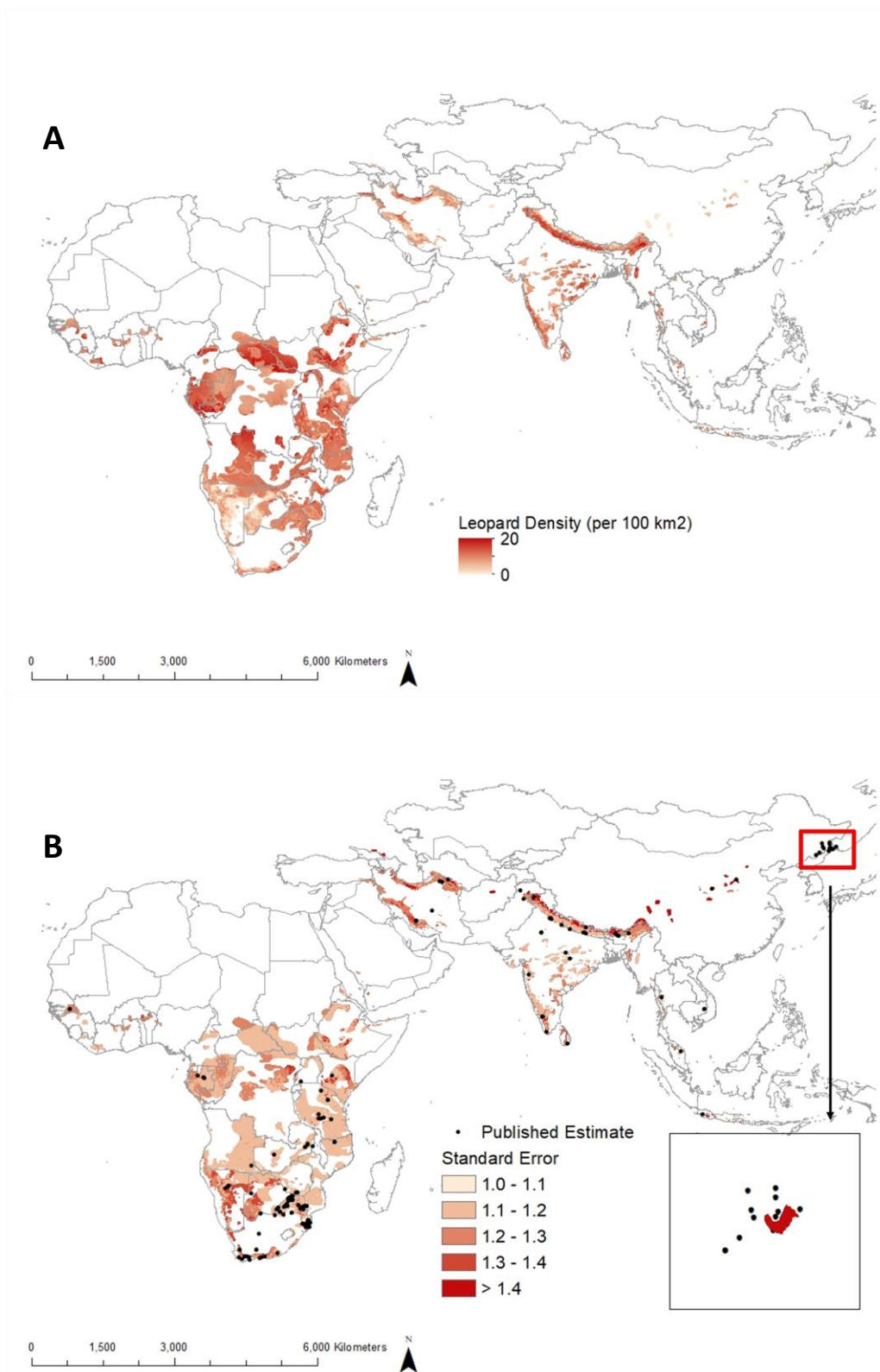


Figure 2.3. Within extant leopard range as defined by Jacobson et al. (2016), shown is the predicted leopard density (individuals/100 km²) from my top model (A) as well as uncertainty expressed as the standard error in predicted leopard density (B). The data used to fit the model also shown (B).

LITERATURE CITED

- Allen ML, Wang S, Olson LO, et al (2020) Counting cats for conservation: seasonal estimates of leopard density and drivers of distribution in the Serengeti. *Biodivers Conserv* 29:3591–3608. <https://doi.org/10.1007/s10531-020-02039-w>
- Balme G, Hunter L, Slotow R (2007) Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Anim Behav* 74:589–598. <https://doi.org/10.1016/j.anbehav.2006.12.014>
- Balme G, Rogan M, Thomas L, et al (2019) Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. *Popul Ecol.* <https://doi.org/10.1002/1438-390X.1023>
- Balme GA, Lindsey PA, Swanepoel LH, Hunter LTB (2014) Failure of research to address the rangewide conservation needs of large carnivores: Leopards in South Africa as a case study. *Conserv Lett* 7:3–11. <https://doi.org/10.1111/conl.12028>
- 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. *Anim Conserv* 13:315–323. <https://doi.org/10.1111/j.1469-1795.2009.00342.x>
- Balme GA, Slotow R, Hunter LTB (2009) Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biol Conserv* 142:2681–2690. <https://doi.org/10.1016/j.biocon.2009.06.020>
- Basille M, Moorter B Van, Herfindal I, et al (2013) Selecting habitat to survive: the impact of road density on survival in a large carnivore. *PLoS One* 8:e65493. <https://doi.org/10.1371/journal.pone.0065493>
- Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. *Science*

(80-) 295:2273–2276

Chase Grey JN, Kent VT, Hill RA (2013) Evidence of a high density Population of harvested leopards in a montane environment. *PLoS One* 8:1–11.

<https://doi.org/10.1371/journal.pone.0082832>

Clavero M, García-Reyes A, Fernández-Gil A, et al (2022) Where wolves were: setting historical baselines for wolf recovery in Spain. *Anim Conserv* 1–11.

<https://doi.org/10.1111/acv.12814>

Constant NL, Bell S, Hill RA (2015) The impacts, characterisation and management of human–leopard conflict in a multi-use land system in South Africa. *Biodivers Conserv* 24:2967–

2989. <https://doi.org/10.1007/s10531-015-0989-2>

Creel S (2018) The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecol Lett* 21:947–956.

<https://doi.org/10.1111/ele.12975>

Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation.

Conserv Biol 16:488–502. <https://doi.org/10.1046/j.1523-1739.2002.00386.x>

Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) The unique ecology of human predators. *Science* (80-) 349:858–860

Devens C, Tshabalala T, McManus J, Smuts B (2018) Counting the spots: The use of a spatially explicit capture–recapture technique and GPS data to estimate leopard (*Panthera pardus*)

density in the Eastern and Western Cape, South Africa. *Afr J Ecol* 56:850–859.

<https://doi.org/10.1111/aje.12512>

Dormann CF, Elith J, Bacher S, et al (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography (Cop)* 36:27–46.

<https://doi.org/10.1111/j.1600-0587.2012.07348.x>

du Preez B, Hart T, Loveridge AJ, Macdonald DW (2015) Impact of risk on animal behaviour and habitat transition probabilities. *Anim Behav* 100:22–37.

<https://doi.org/10.1016/j.anbehav.2014.10.025>

Dudley JP, Ginsberg JR, Plumptre AJ, et al (2002) Effects of war and civil strife on wildlife and wildlife habitats. *Conserv Biol* 16:319–329. [https://doi.org/10.1046/j.1523-](https://doi.org/10.1046/j.1523-1739.2002.00306.x)

[1739.2002.00306.x](https://doi.org/10.1046/j.1523-1739.2002.00306.x)

Durant SM, Bashir S, Maddox T, Laurenson MK (2007) Relating long-term studies to conservation practice: The case of the serengeti cheetah project. *Conserv Biol* 21:602–611.

<https://doi.org/10.1111/j.1523-1739.2007.00702.x>

Ellis MM, Ivan JS, Schwartz MK (2014) Spatially Explicit Power Analyses for Occupancy-Based Monitoring of Wolverine in the U.S. Rocky Mountains. *Conserv Biol* 28:52–62.

<https://doi.org/10.1111/cobi.12139>

Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. *Funct Ecol* 21:1003–1015

Farhadinia MS, Rostro-García S, Feng L, et al (2021) Big cats in borderlands: Challenges and implications for transboundary conservation of Asian leopards. *Oryx* 55:452–460.

<https://doi.org/10.1017/S0030605319000693>

Gaston KJ, Blackburn TM, Greenwood JJD, et al (2000) Abundance–Occupancy Relationships. *J Appl Ecol* 37:39–59

Gaston KJ, Fuller RA (2009) The sizes of species' geographic ranges. *J Appl Ecol* 46:1–9.

<https://doi.org/10.1111/j.1365-2664.2008.01596.x>

Gavashelishvili A, Lukarevskiy V (2008) Modelling the habitat requirements of leopard *Panthera*

- pardus in west and central Asia. *J Appl Ecol* 45:579–588. <https://doi.org/10.1111/j.1365-2664.2007.01432.x>
- Gebretensae K, Kebede F (2022) Review of the status of African lion (*Panthera leo*) in Ethiopia. *Int J Biodivers Conserv* 14:94–102. <https://doi.org/10.5897/IJBC2022.1553>
- Goldberg JF, Tempa T, Norbu N, et al (2015) Examining temporal sample scale and model choice with spatial capture-recapture models in the common leopard *panthera pardus*. *PLoS One* 10:1–20. <https://doi.org/10.1371/journal.pone.0140757>
- Harihar A, Pandav B, Goyal SP (2011) Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *J Appl Ecol* 48:806–814. <https://doi.org/10.1111/j.1365-2664.2011.01981.x>
- Havmøller RW, Tenan S, Scharff N, Rovero F (2019) Reserve size and anthropogenic disturbance affect the density of an African leopard (*Panthera pardus*) meta-population. *PLoS One* 14:e0209541. <https://doi.org/10.1371/journal.pone.0209541>
- Hebblewhite M, Miquelle DG, Murzin AA, et al (2011) Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biol Conserv* 144:2403–2413. <https://doi.org/10.1016/j.biocon.2011.03.020>
- Holt AR, Gaston KJ, He F (2002) Occupancy-abundance relationships and spatial distribution: a review. *Basic Appl Ecol* 3:1–13
- Jacobson AP, Gerngross P, Lemeris Jr. JR, et al (2016) Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ*. <https://doi.org/10.7717/peerj.1974>
- Jędrzejewski W, Robinson HS, Abarca M, et al (2018) Estimating large carnivore populations at global scale based on spatial predictions of density and distribution - application to the

jaguar (*Panthera onca*). PLoS One 13:1–25. <https://doi.org/10.1371/journal.pone.0194719>

Johnston A, Fink D, Reynolds MD, et al (2015) Abundance models improve spatial and temporal prioritization of conservation resources. *Ecol Appl* 25:1749–1756

Jones JPG (2011) Monitoring species abundance and distribution at the landscape scale. *J Appl Ecol* 48:9–13. <https://doi.org/10.1111/j.1365-2664.2010.01917.x>

Kalle R, Ramesh T, Qureshi Q, Sankar K (2011) Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture-recapture sampling. *Acta Theriol (Warsz)* 56:335–342. <https://doi.org/10.1007/s13364-011-0038-9>

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862. [https://doi.org/10.1890/0012-9658\(1998\)079\[2852:EOTDII\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2)

Kowalczyk R, Górny M, Schmidt K (2015) Edge effect and influence of economic growth on Eurasian lynx mortality in the Białowieża Primeval Forest, Poland. *Mammal Res* 60:3–8. <https://doi.org/10.1007/s13364-014-0203-z>

Leroux SJ, Krawchuk MA, Schmiegelow F, et al (2010) Global protected areas and IUCN designations: Do the categories match the conditions? *Biol Conserv* 143:609–616. <https://doi.org/10.1016/j.biocon.2009.11.018>

Llaneza L, Sazatornil V, López-Bao JV (2018) The importance of fine-scale breeding site selection patterns under a landscape-sharing approach for wolf conservation. *Biodivers Conserv* 27:1239–1256. <https://doi.org/10.1007/s10531-017-1491-9>

Loveridge AJ, Sousa LL, Cushman S, et al (2022a) Where have all the lions gone ? Establishing realistic baselines to assess decline and recovery of African lions. 1–15.

<https://doi.org/10.1111/ddi.13637>

Loveridge AJ, Sousa LL, Seymour-Smith JL, et al (2022b) Environmental and anthropogenic drivers of African leopard *Panthera pardus* population density. *Biol Conserv* 272:109641.

<https://doi.org/10.1016/j.biocon.2022.109641>

Marker LL, Dickman AJ (2005) Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *African J Wildl Res* 35:105–115

Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP (2009) Habitat selection at multiple scales. *Écoscience* 16:238–247. <https://doi.org/10.2980/16-2-3238>

McGarigal K, Wan HY, Zeller KA, et al (2016) Multi-scale habitat selection modeling: a review and outlook. *Landsc Ecol* 31:1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>

McManus J, Marshal JP, Keith M, et al (2021) Factors predicting habitat use by leopards in human-altered landscapes. *J Mammal* 102:1473–1483.

<https://doi.org/10.1093/jmammal/gyab110>

Mduma SAR, Sinclair ARE, Hilborn R (1999) Food regulates the Serengeti wildebeest: A 40-year record. *J Anim Ecol* 68:1101–1122. <https://doi.org/10.1046/j.1365-2656.1999.00352.x>

Mishra RP, Mandal D, Basak K, et al (2017) Status of leopard *Panthera pardus* and striped hyena *Hyaena hyaena* and their prey in Achanakmar Tiger Reserve, Central India. *J Zool Stud* 4:34–41

Mukeka JM, Ogutu JO, Kanga E, Røskoft E (2019) Human-wildlife conflicts and their correlates in Narok County, Kenya. *Glob Ecol Conserv* 18:e00620.

<https://doi.org/10.1016/j.gecco.2019.e00620>

Nichols JD, Williams BK (2006) Monitoring for conservation. *Trends Ecol Evol* 21:668–673

Noor A, Mir ZR, Veeraswami GG, Habib B (2020) Density of leopard in a moist-temperate

- forest of western Himalaya, India. *Trop Ecol* 61:301–310. <https://doi.org/10.1007/s42965-020-00090-w>
- Nyhus PJ (2016) Human-wildlife conflict and coexistence. *Annu Rev Environ Resour* 41:143–171. <https://doi.org/10.1146/annurev-environ-110615-085634>
- Odden M, Athreya V, Rattan S, Linnell JDC (2014) Adaptable neighbours: Movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS One* 9:. <https://doi.org/10.1371/journal.pone.0112044>
- Oriol-Cotterill A, Valeix M, Frank LG, et al (2015) Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* 124:1263–1273. <https://doi.org/10.1111/oik.02224>
- Packer C, Brink H, Kissui BM, et al (2011) Effects of trophy hunting on lion and leopard populations in Tanzania. *Conserv Biol* 25:142–153. <https://doi.org/10.1111/j.1523-1739.2010.01576.x>
- Pettorelli N, Ryan S, Mueller T, et al (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Clim. Res.* 46:15–27
- Ramesh T (2010) Prey selection and food habits of large carnivores: tiger *Panthera tigris*, leopard *Panthera pardus* and dhole *Cuon alpinus* in Mudumalai Tiger Reserve, Tamil Nadu
- Rather TA, Kumar S, Khan JA (2020) Multi-scale habitat modelling and predicting change in the distribution of tiger and leopard using random forest algorithm. *Sci Rep* 10:. <https://doi.org/10.1038/s41598-020-68167-z>
- Rather TA, Kumar S, Khan JA (2021) Density estimation of tiger and leopard using spatially explicit capture-recapture framework. *PeerJ* 9:1–16. <https://doi.org/10.7717/peerj.10634>
- Riley SJ, DeGloria SD, Elliot R (1999) A terrain ruggedness index that quantifies topographic

heterogeneity. *Intermt J Sci* 5:23–27

Rodríguez-Recio M, Burgos T, Krofel M, et al (2022) Estimating global determinants of leopard home range size in a changing world. *Anim Conserv* 25:748–758.

<https://doi.org/10.1111/acv.12777>

Rogan MS, Distiller G, Balme GA, et al (2022) Troubled spots: Human impacts constrain the density of an apex predator inside protected areas. *Ecol Appl* 32:1–15.

<https://doi.org/10.1002/eap.2551>

Rosenblatt E, Creel S, Becker MS, et al (2016) Effects of a protection gradient on carnivore density and survival: An example with leopards in the Luangwa valley, Zambia. *Ecol Evol* 6:3772–3785. <https://doi.org/10.1002/ece3.2155>

Sanderson EW, Jaiteh M, Levy MA, et al (2002) The human footprint and the last of the wild.

Bioscience 52:891–904. [https://doi.org/10.1641/0006-](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)

[3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)

Searle CE, Smit J, Strampelli P, et al (2021) Leopard population density varies across habitats and management strategies in a mixed-use Tanzanian landscape. *Biol Conserv* 257:109120.

<https://doi.org/10.1016/j.biocon.2021.109120>

Sharma RK, Jhala Y, Qureshi Q, et al (2010) Evaluating capture-recapture population and density estimation of tigers in a population with known parameters. *Anim Conserv* 13:94–

103. <https://doi.org/10.1111/j.1469-1795.2009.00305.x>

Simcharoen S, Barlow ACD, Simcharoen A, Smith JLD (2008) Home range size and daytime habitat selection of leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Biol*

Conserv 141:2242–2250. <https://doi.org/10.1016/j.biocon.2008.06.015>

Sims DA, Rahman AF, Cordova VD, et al (2006) On the use of MODIS EVI to assess gross

- primary productivity of North American ecosystems. *J Geophys Res Biogeosciences* 111:1–16. <https://doi.org/10.1029/2006JG000162>
- Srivathsa A, Banerjee A, Banerjee S, et al (2022) Chasms in charismatic species research: Seventy years of carnivore science and its implications for conservation and policy in India. *Biol Conserv* 273:109694. <https://doi.org/10.1016/j.biocon.2022.109694>
- Stein AB, Athreya V, Gerngross P, et al (2020) *Panthera pardus* (amended version of 2019 assessment). *IUCN Red List Threat Species* 2020 8235:e.T15954A163991139
- Stein AB, Fuller TK, DeStefano S, Marker LL (2011) Leopard population and home range estimates in north-central Namibia. *Afr J Ecol* 49:383–387. <https://doi.org/10.1111/j.1365-2028.1990.tb01148.x>
- Steinmetz R, Seuaturien N, Chutipong W (2013) Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biol Conserv* 163:68–78. <https://doi.org/10.1016/j.biocon.2012.12.016>
- Suraci JP, Nickel BA, Wilmers CC (2020) Fine-scale movement decisions by a large carnivore inform conservation planning in human-dominated landscapes. *Landsc Ecol* 35:1635–1649. <https://doi.org/10.1007/s10980-020-01052-2>
- Swanepoel LH, Lindsey P, Somers MJ, et al (2013) Extent and fragmentation of suitable leopard habitat in South Africa. *Anim Conserv* 16:41–50. <https://doi.org/10.1111/j.1469-1795.2012.00566.x>
- Swanepoel LH, Somers MJ, Dalerum F (2015) Density of leopards *Panthera pardus* on protected and non-protected land in the Waterberg Biosphere, South Africa. *Wildlife Biol* 21:263–268. <https://doi.org/10.2981/wlb.00108>
- Tilman D, Clark M, Williams DR, et al (2017) Future threats to biodiversity and pathways to

- their prevention. *Nature* 546:73–81. <https://doi.org/10.1038/nature22900>
- Ugbaje SU, Odeh IOA, Bishop TFA, Li J (2017) Assessing the spatio-temporal variability of vegetation productivity in Africa: quantifying the relative roles of climate variability and human activities. *Int J Digit Earth* 10:879–900. <https://doi.org/10.1080/17538947.2016.1265017>
- Valeix M, Loveridge AJ, Davidson Z, et al (2010) How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landsc Ecol* 25:337–351. <https://doi.org/10.1007/s10980-009-9425-x>
- Vinks MA, Creel S, Rosenblatt E, et al (2022) Leopard *Panthera pardus* density and survival in an ecosystem with depressed abundance of prey and dominant competitors. *Oryx* 56:518–527. <https://doi.org/10.1017/S0030605321000223>
- Vitkalova A V., Feng L, Rybin AN, et al (2018) Transboundary cooperation improves endangered species monitoring and conservation actions: A case study of the global population of Amur leopards. *Conserv Lett* 11:1–8. <https://doi.org/10.1111/conl.12574>
- Wang T, Andrew Royle J, Smith JLD, et al (2018) Living on the edge: Opportunities for Amur tiger recovery in China. *Biol Conserv* 217:269–279. <https://doi.org/10.1016/j.biocon.2017.11.008>
- Weber W, Rabinowitz A (1996) A global perspective on large carnivore conservation. *Conserv Biol* 10:1046–1054. <https://doi.org/10.1046/j.1523-1739.1996.10041046.x>
- Wolf C, Ripple WJ (2017) Range contractions of the world’s large carnivores. *R Soc Open Sci* 4:. <https://doi.org/10.1098/rsos.170052>
- Woodroffe R (2000) Predators and people: using human densities to interpret declines of large

carnivores. *Anim Conserv* 3:165–173. <https://doi.org/10.1017/S136794300000086X>

Zafar-ul Islam M, Boug A, Judas J, As-Shehri A (2018) Conservation challenges for the Arabian Leopard (*Panthera pardus nimr*) in the Western Highlands of Arabia. *Biodiversity* 19:188–197. <https://doi.org/10.1080/14888386.2018.1507008>

CONCLUSIONS

Despite growing recognition of the importance of observation scale on study outcomes (Wiens 1989; Levin 1992), my work shows that many studies of human-carnivore conflict, specifically carnivore depredation studies, still fail to report either standard conflict metrics or effective estimates of spatial and temporal scale. Both these deficiencies interfere with gaining useful inference from cross-study comparisons. For those studies that did report sufficient information for comparison, human-carnivore conflict metrics exhibited a generally linear relationship with observation scale. The total number of animals killed and attack incidents increased with spatiotemporal extent, whereas percent annual loss of stock decreased across both broader spatial extents and temporal durations. There was also evidence of nonlinearity in the spatial scaling of the number of attack incidents. Understanding such scaling relationships will inform more robust aggregation of data from diverse socioecological contexts, enabling clearer inference when seeking effective conservation actions. Moreover, scale has an effect not only on observations of human-carnivore interactions, but also on the association between such observations and other variables. Using leopards as an example, estimated densities of this species varied with spatial scale of the study (a design effect), which I controlled for to elucidate the effects of environmental (temperature, productivity, land cover, water) and anthropogenic (human density) drivers. Spatial drivers were most predictive of leopard density over relative fine (1 or 5 km) to broad (20 km) scales, and several relationships were non-linear. Overall, the scale-dependent nature of ecological processes has been well documented, although until now this knowledge has only been scantily applied to global consideration of large carnivores. Further, where scale is considered, extent is far more commonly reported than resolution despite evidence that the spatial and temporal grain of observation influences prediction uncertainty and relationships

between variables. There are still many fertile areas for research moving forward, including elucidating which spatiotemporal drivers are contributing to high uncertainty in human-carnivore conflict observations across both extent and resolution, and understanding how socioecological processes interact across scales to produce observed patterns. And for future cross-study comparisons, I've made several recommendations for how local studies can contribute more reliable information to enable corrections for scaling effects and, by extension, contribute more directly to effective conservation actions for large carnivores.

APPENDICES

Appendix 1.1a. Components of spatial and temporal extent models

Model name in subsequent Appendices*	Components
null	NA
spatial	Spatial Extent
spatial_quadratic	$\text{Spatial Extent}^2 + \text{Human Density}^2$
only_spatial_quadratic	Spatial Extent^2
temporal	Temporal Extent
temporal_quadratic	$\text{Temporal Extent}^2 + \text{Human Density}^2$
only_temporal_quadratic	Temporal Extent^2
full	$\text{Spatial Extent} + \text{Temporal Extent} + \text{Spatial Extent} * \text{Temporal Extent} + \text{Spatial Extent} * \text{Human Density} + \text{Spatial Extent} * \text{Carnivore Mass}$
full_quadratic	$\text{Spatial Extent}^2 + \text{Temporal Extent}^2 + \text{Human Density}^2 + \text{Spatial Extent} * \text{Temporal Extent} + \text{Spatial Extent} * \text{Human Density} + \text{Spatial Extent} * \text{Carnivore Mass}$
interactions_spatial_temporal	$\text{Spatial Extent} * \text{Temporal Extent}$
interactions_spatial_mass	$\text{Spatial Extent} * \text{Carnivore Mass}$
interactions_spatial_density	$\text{Spatial Extent} * \text{Human Density}$
interactions_temporal_mass	$\text{Temporal Extent} * \text{Carnivore Mass}$
interactions_temporal_density	$\text{Temporal Extent} * \text{Human Density}$

*Human density and carnivore body mass are included in each model, including the null, not explicitly listed here.

Appendix 1.1b. Components of spatial and temporal resolution models

Model name in subsequent Appendices*	Components
null	NA
full	Temporal Extent + Temporal Extent*Temporal Resolution
spatial	Spatial Extent
temporal	Temporal Extent
only_human_quadratic	Human Density ²
full_quadratic	Human Density ² + Temporal Extent + Temporal Extent*Temporal Resolution
interactions_temporal	Temporal Extent*Temporal Resolution
“sres” or “tres”	Only spatial or temporal resolution

*Apart from the null model, each model also contains either spatial or temporal resolution.

Human density and carnivore body mass are included in each model, including the null, not explicitly listed here.

Appendix 1.2a. AICc model selection results for %loss (total, n = 76). See Appendix 1.1a for model components

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
interactions_spatial_temporal	8	358	0.0	1.0e+00	6.0e-01	-168	0.60
full	11	359	1.5	4.8e-01	2.9e-01	-165	0.89
spatial	6	363	5.7	5.8e-02	3.5e-02	-174	0.93
interactions_spatial_density	7	363	5.8	5.6e-02	3.4e-02	-173	0.96
only_spatial_quadratic	7	365	7.1	2.8e-02	1.7e-02	-173	0.98
full_quadratic	14	365	7.8	2.0e-02	1.2e-02	-164	0.99
interactions_spatial_mass	8	367	8.9	1.1e-02	6.9e-03	-173	1.00
spatial_quadratic	8	367	9.6	8.2e-03	4.9e-03	-173	1.00
temporal	6	455	97.0	8.5e-22	5.1e-22	-220	1.00
only_temporal_quadratic	7	456	98.0	5.3e-22	3.2e-22	-219	1.00
interactions_temporal_mass	8	457	99.0	3.2e-22	1.9e-22	-218	1.00
interactions_temporal_density	7	457	99.0	3.1e-22	1.9e-22	-220	1.00
temporal_quadratic	8	458	100.4	1.6e-22	9.5e-23	-219	1.00
null	5	460	102.0	7.0e-23	4.2e-23	-223	1.00

Appendix 1.2b. AICc model selection results for log(#kills) (total, n = 111). See Appendix 1.1a for model components

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
interactions_temporal_mass	8	427	0.0	1.00000	0.88496	-204	0.88
only_temporal_quadratic	7	433	5.9	0.05144	0.04552	-208	0.93
temporal_quadratic	8	433	6.4	0.04112	0.03639	-207	0.97
temporal	6	435	8.4	0.01518	0.01343	-210	0.98
interactions_temporal_density	7	436	9.2	0.01005	0.00890	-209	0.99
interactions_spatial_temporal	8	438	10.8	0.00454	0.00402	-209	0.99
full	11	440	12.7	0.00174	0.00154	-206	0.99
null	5	440	13.3	0.00132	0.00117	-214	1.00
only_spatial_quadratic	7	441	13.9	0.00097	0.00086	-212	1.00
full_quadratic	14	441	14.0	0.00093	0.00083	-203	1.00
spatial_quadratic	8	441	14.2	0.00085	0.00075	-211	1.00
spatial	6	441	14.2	0.00083	0.00073	-213	1.00
interactions_spatial_mass	8	441	14.5	0.00072	0.00064	-211	1.00
interactions_spatial_density	7	443	16.2	0.00031	0.00028	-213	1.00

Appendix 1.2c. AICc model selection results for log(#attacks) (total, n = 62). See Appendix 1.1a for model components

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
interactions_temporal_density	7	242	0.00	1.0000	0.2517	-111	0.25
spatial_quadratic	8	242	0.11	0.9457	0.2381	-110	0.49
temporal_quadratic	8	242	0.38	0.8263	0.2080	-110	0.70
interactions_spatial_temporal	8	243	1.77	0.4127	0.1039	-111	0.80
only_temporal_quadratic	7	244	2.39	0.3026	0.0762	-113	0.88
temporal	6	245	3.03	0.2203	0.0555	-114	0.93
only_spatial_quadratic	7	246	4.15	0.1256	0.0316	-114	0.96
null	5	247	5.18	0.0750	0.0189	-117	0.98
spatial	6	249	7.10	0.0288	0.0072	-116	0.99
interactions_temporal_mass	8	250	8.08	0.0176	0.0044	-114	1.00
interactions_spatial_mass	8	251	9.38	0.0092	0.0023	-115	1.00
interactions_spatial_density	7	251	9.45	0.0089	0.0022	-116	1.00

Appendix 1.3a. AICc model selection results for %loss (temporal resolution). See Appendix 1.1b for model components

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
spatial	9	338	0	1.0e+00	1.0e+00	-157	1
temporal	9	395	57	4.8e-13	4.8e-13	-185	1
tres	8	398	60	9.8e-14	9.8e-14	-188	1
only_human_quadratic	9	400	63	2.5e-14	2.5e-14	-188	1
full	12	401	63	1.8e-14	1.8e-14	-184	1
full_quadratic	13	404	66	4.0e-15	4.0e-15	-184	1
null	5	554	216	1.3e-47	1.3e-47	-270	1

Appendix 1.3b. AICc model selection results for log(#kills) (temporal resolution). See Appendix 1.1b for model components

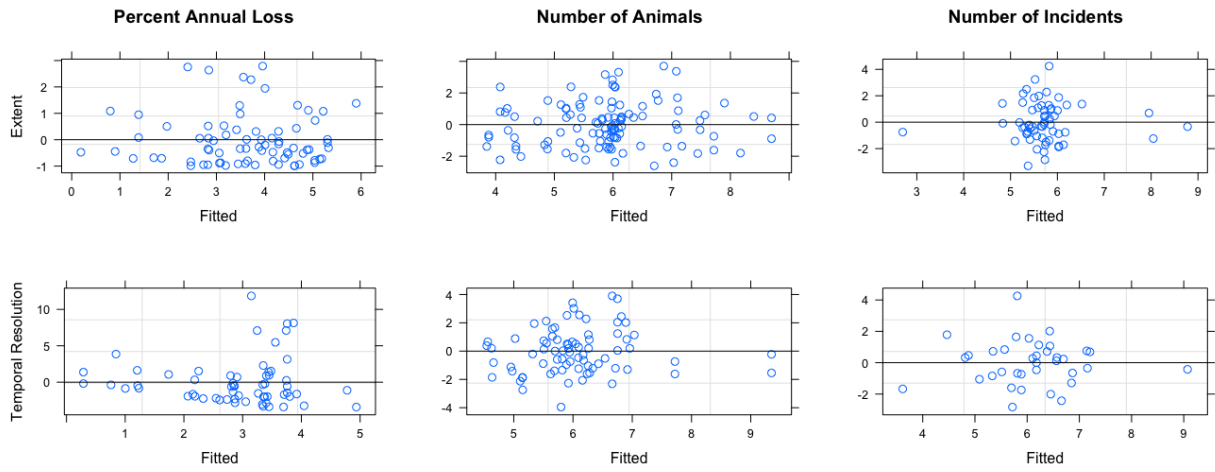
Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
temporal	9	321	0.00	1.0e+00	2.1e-01	-149	0.21
tres	8	321	0.15	9.3e-01	2.0e-01	-150	0.41
only_human_quadratic	9	321	0.38	8.2e-01	1.8e-01	-149	0.59
spatial	9	321	0.54	7.6e-01	1.6e-01	-149	0.75
full	12	322	0.94	6.2e-01	1.3e-01	-145	0.89
full_quadratic	13	322	1.28	5.3e-01	1.1e-01	-144	1.00
null	5	440	119.43	1.2e-26	2.5e-27	-214	1.00

Appendix 1.3c. AICc model selection results for log(#attacks) (temporal resolution). See

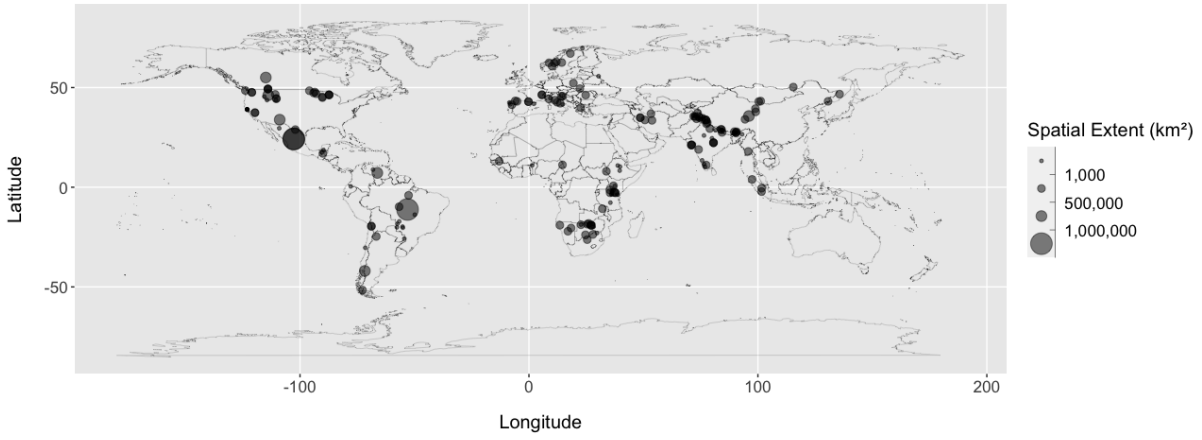
Appendix 1.1b for model components

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
temporal	9	154	0.0	1.0e+00	6.7e-01	-63	0.67
tres	8	156	2.2	3.4e-01	2.2e-01	-66	0.89
interactions_temporal	12	159	4.5	1.1e-01	7.2e-02	-58	0.96
spatial	9	160	5.8	5.4e-02	3.6e-02	-66	1.00
null	5	247	92.6	7.7e-21	5.1e-21	-117	1.00

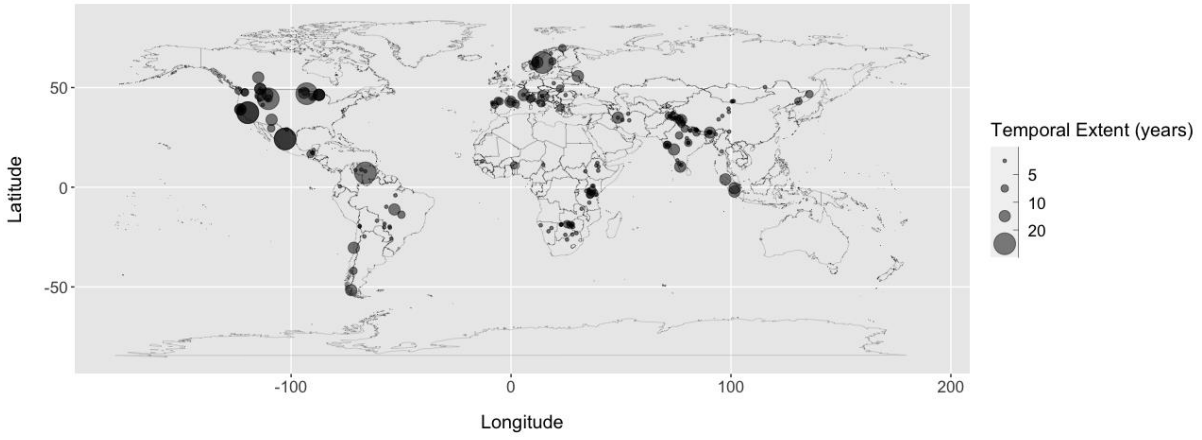
Appendix 1.4. Residual plots of single top models fit to the three metrics of conflict



Appendix 1.5a. Studies plotted according to their latitude and longitude values, and symbolized by spatial extent (km²)



Appendix 1.5b. Studies plotted according to their latitude and longitude values, and symbolized by temporal extent (years)



Appendix 2.1. Description of land cover classes as derived from MODIS MCD12Q1 and collapsed classes used for predicting leopard density.

Initial class	Description	Collapsed class
Barren	≥60% non-vegetated/barren (sand, rock, soil) or permanent snow/ice, <10% vegetation	Not encountered (ultimately masked from predictions)
Permanent Snow & Ice	≥60% covered by snow and ice for at least 10 months of the year	Not encountered (ultimately masked from predictions)
Water Bodies	≥60% covered by permanent water bodies	Not encountered (ultimately masked from predictions)
Urban & Built-Up Lands	≥30% made up of impervious surfaces including building materials, asphalt, and vehicles	Shrub / urban
Dense Forests	Tree cover >60% (canopy >2m height)	Dense forest / cropland
Open Forests	Tree cover 10-60% (canopy >2m height)	Reference
Forest/Cropland Mosaics	Mosaics of small-scale cultivation (40-60%) with >10% natural tree cover	Dense forest / cropland
Natural Herbaceous	Dominated by herbaceous annuals (<2m), ≥10% cover	Reference
Natural Herbaceous/Croplands Mosaics	Mosaics of small-scale cultivation (40-60%) with natural shrub or herbaceous vegetation	Dense forest / cropland
Herbaceous Croplands	Dominated by herbaceous annuals (<2m), ≥60% cover, >60% cultivated	Dense forest / cropland
Shrublands	>60% shrub cover (1-2m height)	Shrub / urban

Appendix 2.2. Spatial data sources used to derive environmental variables for the leopard density models.

Data name	Resolution	Source
Human population density (2010)	1 km	https://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-adjusted-to-2015-unwpp-country-totals-rev11
Human footprint index (2009)	1 km	https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint
Terrain ruggedness (2010)	1 km	https://www.usgs.gov/coastal-changes-and-impacts/gmted2010
Categorical land cover type (band used is LC_Prop2, average from 2001 to 2022)	500 m	https://lpdaac.usgs.gov/products/mcd12c1v061/
Enhanced vegetation index (average from 2000 to 2017)	500 m	https://developers.google.com/earth-engine/datasets/catalog/MODIS_MCD43A4_006_EVI
Normalized difference vegetation index (average from 2000 to 2017)	500 m	https://developers.google.com/earth-engine/datasets/catalog/MODIS_MCD43A4_006_NDVI
Normalized difference water index (average from 2000 to 2017)	500 m	https://developers.google.com/earth-engine/datasets/catalog/MODIS_MCD43A4_006_NDWI
Mean annual temperature (bioclimatic variables, average from 1970 to 2000)	1 km	https://www.worldclim.org/data/worldclim21.html
Mean annual precipitation (bioclimatic variables, average from 1970 to 2000)	1 km	https://www.worldclim.org/data/worldclim21.html
Mean forest canopy cover (average from 2000 to 2020)	250 m	https://lpdaac.usgs.gov/products/mod44bv006/
Gross primary productivity (average from 2000 to 2022)	500 m	https://lpdaac.usgs.gov/products/mod17a2h-v006/

Net primary productivity
(average from 2000 to 2022)

500 m

https://lpdaac.usgs.gov/products/mod17a3h_gfv006/

Appendix 2.3. Plausible candidate models for predicting log(density) of leopard (*Panthera pardus*). An “x” in a shaded cell indicates the model included that variable. All models (including the null) also included 4 design-based covariates not shown here (i.e., area sampled, number of study days, number of camera sites, and number of trap nights).

Model	Predictor variable												
	Temperature	Temperature quadratic term (x ²)	Precipitation	Human density	Human footprint	Terrain Ruggedness Index (TRI)	Normalized Difference Water Index (NDWI)	Enhanced Vegetation Index (EVI)	Gross Primary Productivity (GPP)	GPP quadratic term (x ²)	Land cover class (3 types)	Continent Indicator (1 = Africa, 0 = Asia)	Protected area (PA)
Null													
Global (Full)	X	X	X	X	X	X	X	X	X	X	X	X	X
Human impact				X	X						X	X	X
Environmental	X	X	X			X	X	X	X	X	X	X	X
Global – indicator variable	X	X	X	X	X	X	X	X	X	X	X		
Global – protected area	X	X	X	X	X	X	X	X	X	X	X	X	
Global – NDWI	X	X	X	X	X	X		X	X	X	X	X	X
Global – EVI	X	X	X	X	X	X	X		X	X	X	X	X
Global – GPP	X	X	X	X	X	X	X	X			X	X	X
Global – temperature			X	X	X	X	X	X	X	X	X	X	X
Global – precipitation	X	X		X	X	X	X	X	X	X	X	X	X
Global – human density	X	X	X		X	X	X	X	X	X	X	X	X
Global – human footprint	X	X	X	X		X	X	X	X	X	X	X	X
Global – TRI	X	X	X	X	X		X	X	X	X	X	X	X
Global – land cover	X	X	X	X	X	X	X	X	X	X		X	X

Global – temperature and precipitation
 Global – quadratic terms
 Global – quadratic temperature
 Global – quadratic GPP

			X	X	X	X	X	X	X	X	X	X
X		X	X	X	X	X	X	X		X	X	X
X		X	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X		X	X	X

SANDY AURORA SLOVIKOSKY

Address: 908 Harrison Street, Apt. #119, Syracuse, NY 13210

Phone: (520) 499-4228

Email: saslovik@syr.edu

Website: <https://sanimal.net>

LinkedIn: www.linkedin.com/in/sandy-slovikosky

ResearchGate: https://www.researchgate.net/profile/Sandy_Slovikosky

EDUCATION

- State University of New York College of Environmental Science and Forestry, Syracuse, New York (Fall 2020 – Spring 2023)
 - Master of Science in Environmental Biology: Wildlife Ecology and Management. Thesis: A Global Assessment of Drivers of Carnivore-Human Conflict and Leopard (*Panthera pardus*) Density.
- University of Arizona, Tucson, Arizona (Fall 2016 – Spring 2020)
 - Bachelor of Science in Natural Resources: Wildlife Conservation and Management. Graduated Summa Cum Laude.

EMPLOYMENT EXPERIENCE

- SUNY College of Environmental Science and Forestry, Syracuse, NY - *Graduate Teaching Assistant (Fall 2020 – Spring 2022)*

- Research Foundation for the State University of New York, Syracuse, NY - *Senior Research Aide (Summer 2021)*
- University of Arizona, Tucson, AZ - *Undergraduate Research Assistant (Fall 2018 – Spring 2020)*

VOLUNTEER EXPERIENCE

- University of Arizona Student Chapters of the American Fisheries Society and The Wildlife Society, Tucson, AZ - *President (2019)*
- SUNY College of Environmental Science and Forestry Student Chapter of The Wildlife Society, Syracuse, NY - *Graduate Advisor (Fall 2022 – Spring 2023)*
- Wildlife ACT, Zululand, South Africa - *Student Intern (Summer 2018)*
- University of Arizona, Tucson, AZ - *Preceptor for College Botany (Fall 2017)*
- SUNY College of Environmental Science and Forestry Graduate Student Association, Syracuse, NY - *Department Representative (Fall 2021 – Summer 2022)*
- Southern Arizona Research, Science, and Engineering Fair, Tucson, AZ - *Grand Awards Judge (Spring 2018, 2019, 2020)*
- Tucson Wildlife Center, Tucson, AZ - *Bird Care Volunteer (Summer 2017)*

PUBLICATIONS

- Slovikosky, S.A., Merrick, M.J., Morandini, M., and Koprowski, J.L. 2022. **Small mammal movement response to burn severity reveals importance of microhabitat features.** Journal of Mammalogy, under review.

ORAL/POSTER PRESENTATIONS

- Slovikosky, S.A., Frair, J.L., Petracca, L.S., and Hunter, L. November 2022.
Scaling issues in the study of livestock depredation by carnivores. Oral presentation. The Wildlife Society 29th Annual Conference, Spokane, WA.
- Slovikosky, S.A., Frair, J.L., Petracca, L.S., and Hunter, L. June 2022.
Scaling issues in the study of livestock depredation by carnivores. Oral presentation. American Society of Mammalogists 101st Annual Meeting, Tucson, AZ.
- Slovikosky, S.A., Frair, J.L., Petracca, L.S., and Hunter, L. November 2021.
Scaling issues in the study of livestock depredation by carnivores. Poster presentation. The Wildlife Society 28th Annual Conference, virtual.
- Slovikosky, S.A., Merrick, M.J., Morandini, M., and Koprowski, J.L. June 2021.
Small mammal movement response to burn severity in a mixed conifer forest. Oral presentation. American Society of Mammalogists 100th Annual Meeting, virtual.
- Slovikosky, S.A., Koprowski, J.L., and Merrick, M.J. September 2020. **Small mammal movement response to burn severity in a mixed conifer forest.** Oral presentation. The Wildlife Society 27th Annual Conference, virtual.
- Slovikosky, S.A., and Koprowski, J.L. January 2020. **Assessing Mexican**

woodrat *Neotoma mexicana* movement over patches of different burn severity. Poster presentation. 53rd Joint Annual Meeting, AZ/NM Chapters of the American Fisheries Society and The Wildlife Society, Prescott, AZ.

- Slovikosky, S.A., and Koprowski, J.L. January 2020. **Assessing Mexican woodrat *Neotoma mexicana* movement over patches of different burn severity.** Poster presentation. University of Arizona Undergraduate Biology Research Program 31st Annual Conference, Tucson, AZ.

FEATURED ARTICLES

- Slovikosky, S.A. **Interview: Collaborating with an open mind to conserve wildlife globally and at home.** International Wildlife Management Working Group of The Wildlife Society Newsletter. February 2021.
- Slovikosky, S.A. **Radiant rodents.** Arizona Chapter of The Wildlife Society Winter Newsletter. January 2020.
- Slovikosky, S.A. **Experiencing history: the largest gathering of fish and wildlife professionals ever.** University of Arizona Undergraduate Biology Research Program Newsletter. January 2020.
- Slovikosky, S.A. **UA student tracks pack rats in the wild using fluorescent powder.** Arizona Daily Star, Tucson Newspaper. September 2019.
- Slovikosky, S.A. **Packrats and their importance to biodiversity.** The Daily Wildcat, University of Arizona Newspaper. September 2019.
- Slovikosky, S.A. **Wildlife ACT: South Africa's growing hope in conservation.** Arizona Chapter of The Wildlife Society Winter Newsletter. January 2019.
- Slovikosky, S.A. **Spotlight your research: create a blog.** Arizona Chapter of

AWARDS AND ACHIEVEMENTS

- National Science Foundation Graduate Research Fellowship Program Honorable Mention 2020.
- American Society of Mammalogists Undergraduate Honorarium 2020.
- SUNY ESF Graduate Student Association Excellence in Teaching Award 2021.
- SUNY ESF Tuition Scholarship 2020-22.
- University of Arizona Wildcat Excellence Scholarship 2016-20.
- Member of Phi Beta Kappa.
- Class of 2020 Commencement Speaker, College of Agriculture and Life Sciences, University of Arizona.
- Associate Wildlife Biologist Certification (The Wildlife Society).

PROFESSIONAL MEMBERSHIPS

- The Wildlife Society.
- American Society of Mammalogists.
- Wild Felid Research and Management Association.