Large Carnivores: Case studies on nonlethal effects, population monitoring, and responses to prey depletion

By

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Executive Summary

Large carnivores make up a globally threatened group of culturally, politically, and ecologically important species. While the ecology of these species can differ wildly, from the solitary and omnivorous American black bear inhabiting North American woodlands to the gregarious and obligate carnivorous African lion stalking the grasslands across Sub-Saharan Africa, there are shared points of research and management interest across these taxa. Crucial research foci for all large carnivores include transparent and scientific population monitoring practices, top-down effects on the ecosystems they inhabit, and evaluating threats to their persistence. Therefore, I addressed my dissertation as an opportunity to investigate aspects of each of these concerns for gray wolves (Canis lupus) in Wisconsin and Amur tigers (Panthera tigris tigris) in Russia, and applied the results to recommendations for important, future avenues of study and intervention.

In my first chapter, I analyzed how Wisconsin counted individual gray wolves between 2003-11. I described the methodological changes in Wisconsin wolf-censusing techniques by the Wisconsin Department of Natural Resources and hypothesize how changes to volunteer training and participation in winter wolf counts may have resulted in several methodologically distinct time series of wolf population estimates, rather than a single time series as the state has often used. I analyzed how volunteers and DNR counted wolves with a mixed effects model during years of methodological consistency and found evidence in support of volunteers counting fewer wolves than DNR trackers from winters 2003-11, implying that changes in volunteer censusing before and after that period must necessarily affect the bias and precision of wolf population estimates. I end with recommendations for more transparent and reproducible wolf counting by the WDNR.

In my second chapter, I focused on one subset of potential effects of a large carnivore on its ecosystem when I investigated potential nonlethal effects of Amur tigers on ungulate prey in the Russian Far East. Motivated by previous studies on tiger kill-site selection and nonlethal effects of wolves and lynx in Poland, I set up an experiment in Sikhote-Alin Biosphere Zapovednik (SABZ) to test the potential behavioral effects of olfactory cues of tiger presence on ungulate prey species, including wild boar (Sus scrofa), sika deer (Cervus nippon) and red deer (Cervus canadensis). I hypothesized that ungulate prey would exhibit antipredator behaviors such as head-up visual scanning (vigilance), reduced visitation times, decreased foraging, and altered grouping behaviors at sites with cues of tiger presence. At several bait stations in SABZ, I recorded ungulate behavior to analyze whether antipredator behavior increased in the presence of cues of tiger presence. I found evidence that the presence of piglets may increase vigilant behaviors in adult wild boar, indicating that intrinsic group vulnerability may be more important to wild boar antipredator behaviors than indirect cues of predator presence. I also found weakly significant evidence that sensory cues of tigers may increase the duration of wild boar visits to sites. I discuss how this may confound an effect of tiger sensory cues on wild boar vigilance, and I propose follow up research on a broader suite of potential nonlethal effects of tigers.

In my third chapter, I addressed the arrival of African Swine Fever (ASF) in Russia and how resultant drops in wild boar populations could lead to significant wild prey depletion for Amur tigers. As a result of this specific prey depletion, I hypothesized that tiger populations at the northern limits of Amur tiger range, where deer populations are lower, would suffer the greatest change to their local carrying capacity and therefore see the greatest relative change in quasi-extinction risk. Using published estimates of baseline ungulate densities and estimates from SABZ of wild boar mortality under ASF, I estimated carrying capacities at 4 disparate sites across Amur tiger range before ASF and hypothesized three different scenarios for ASF persistence. I then simulated tiger population trajectories with a stochastic stage-structured population model to project relative changes in quasi-extinction risk under

these different ASF scenarios. I found evidence in support of my hypothesis, finding the greatest increase in quasi-extinction risk in simulations for a small, isolated park where wild boar make up over 70% of ungulate biomass. I make recommendations for managers to assess vulnerability for tiger populations inside and outside of protected areas to wild boar prey depletion. I also suggest more complex models that simulate different functional effects of prey depletion on tiger populations.

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This work is dedicated to my family, my friends, Kam, and to tiger U1509m, whom I photographed December 2, 2021 in Sikhote-Alin Biosphere Zapovednik.

Chapter 1

Community Counting Carnivores: Discrepancies between Volunteer and DNR winter gray wolf counts in Wisconsin 2003-2011 with implications for defensible inference

Introduction

Large Carnivores and Population Monitoring

Large carnivores are threatened globally, with most extant taxa having experienced range contractions greater than 50% since historical times (1). Ecologists and conservationists have dedicated renewed efforts towards large carnivore conservation as part of a larger effort to support the top-down regulatory effects of apex predators, a function often filled by large carnivores in terrestrial ecosystems (2). Challenges to large carnivore conservation include competition with local human populations for space and prey, human fear of threats posed by large carnivores to human safety and domestic animals, and economic incentives to kill carnivores and sell their body parts (3–5).

Population monitoring is standard practice among conservation and management decision-makers for assessing the health and trajectory of wild populations, and while many ecologists are increasingly advocating for a more robust suite of demographic parameters to assess population health, such monitoring efforts remains central and critical tools (6–8). Monitoring efforts for large carnivores are expensive and labor-intensive, owing to carnivores often showing cryptic and wide-ranging behaviors; furthermore, these species are often both charismatic and polarizing, drawing further attention and scrutiny to conservation and management programs that involve them (9–13).

The biological and human dimensions of large carnivore management make monitoring programs potentially vulnerable to political influence (14). Darimont et al. specifically warned that population metrics of these large carnivore populations can be selectively and inaccurately used by decision makers to serve politically-preferred goals, rather than toward empirically derived goals with explicit and transparent normative bases. They termed this scenario as the creation of a 'political population' (10). While proving the existence of a political population is difficult, case studies involving tigers (*Panthera tigris*) in several Asian range states and gray wolves (*Canis lupus*) in Europe and North America highlight possible examples of political populations of large carnivores(10,13).

Given the background of large carnivores' ecological importance, imperiled status, and the complex political landscape of large carnivore management, it is critical that independent scientists review these management efforts in order to encourage accuracy, transparency, and best practices.

Wisconsin Department of Natural Resources Wolf Census Methods

From at least 1980 through 2020 the Wisconsin Department of Natural Resources (DNR) used three primary methods to census wolf populations: aerial counts of packs with radio-collared individuals, howling surveys, and winter track surveys, with supplementary information sources such as dead wolf recovery, livestock predation investigations, and public observation reports (15,16). DNR provided tables summarizing the data collected from these methods annually, and combined information from these three methods into an annual minimum wolf population estimate via a process of expert opinion and community volunteer data discussed during public meetings. Due to the resulting incomplete documentation on decisions and annually idiosyncratic methods, reported minimum annual wolf counts are not fully reproducible. However, the DNR did report details of the annual winter track surveys in state wolf reports, providing an opportunity for outside analysis.

The winter track survey methods changed during the period from 1994-1996 when the DNR recruited volunteer trackers to aid in the census and changed again between 2000 and 2004 in terms of the training and scrutiny given to volunteer winter track efforts (17–19). Some of the major changes to both the winter tracking program and how wolf populations are estimated are shown in Figure 1. From winter

2003-2004 through winter 2010-2011, DNR reported block by block track survey results for both the volunteers and DNR staff, making it possible to assess uncertainty in winter track surveys, and specifically to assess whether volunteer trackers counted wolves in a quantitatively different manner than their DNR counterparts; if so, the change in relative contributions of volunteers between survey periods would suggest that this surveyor-specific effect should be explicitly accounted for in reporting wolf population estimates, or that changes in methodology set bounds on population time series for analysis. Given that DNR's new occupancy model for assessing wolf abundance still relies upon contributions from winter track surveys, assessing its accuracy and precision remains critical to reliable wolf science and policy (16).

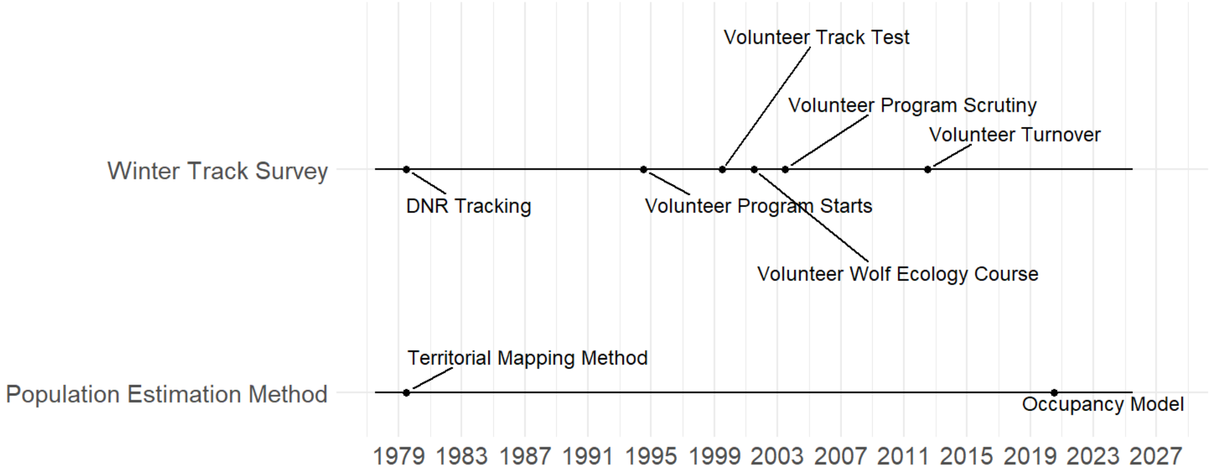


Figure 1: Timeline of major changes to Wisconsin DNR Winter Wolf Track Survey methods and Population Estimation Methods. Due to data availability and methodological consistency, I analyzed the period from winter 2003-04 to 2010-11, between 'Volunteer Program Scrutiny' and 'Volunteer Turnover' (17,19–21).

Volunteer Winter Tracking Program

The specifics of annual volunteer tracking training and outcomes are not fully described in released reports. Namely, we lack information on the exact routes taken by trackers, the specifics of updated training regimes, and as described below, the relative confidence that the DNR had in different classes of volunteer. Further, we do not have information on how blocks were selected to be surveyed by either volunteers, DNR, or both tracker types in a given year. Sampling bias remains among the most common and pernicious forms of scientific bias across disciplines, and without describing either a clearly random sampling method, or scientifically describing and accounting for a non-random scheme, we must remain skeptical about the accuracy, precision, and reproducibility of any results generated in such a way (22,23).

The DNR exercised its own self-scrutiny on the discrepancies between volunteers and DNR trackers (18,24). In a 2003 presentation on integration of volunteer data, they noted additions to training in 1999 (a track test) and 2001 (on wolf ecology) (Figure 1) (18). Between 1975 and 2000, they noted that untrained volunteers surveyed 4604 miles and counted 54% the number of tracks per mile surveyed as DNR counterparts in co-surveyed blocks (defined as same geographic area, same winter, precise route(s) and month unknown), while trained volunteers surveyed 1963 miles and counted 70% of the number of tracks per mile in blocks as DNR counterparts in co-surveyed blocks. The DNR also noticed that different strata of tracking experience for volunteers produced different discrepancies with DNR trackers, with the smallest discrepancy for volunteers with >40 hours of tracking experience (93% the rate of DNR co-trackers) (18).

From presentations and reports at the time, the DNR's conclusions coalesced around the following: 1) Volunteer's ability to detect wolf tracks improves with training and experience; 2) While volunteers may be detecting tracks at lower rates, their overall estimate of wolf populations may be accurate; 3)

Volunteer results can be used for detection of novel wolf presence, in areas not surveyed by the DNR, and to check DNR numbers, all with the understanding that trained, experienced volunteers produce results more consistent with DNR trackers (18,24). However, the specifics of how these directives and suggestions were applied are not reported in state wolf reports, nor was volunteer experience or training level reported on a block-by-block basis.

An Examination of Participatory Science

Beyond this specific case study of state management of a large carnivore population, this study is also an opportunity to add to the growing body of literature on large scale participatory monitoring efforts. Participation of non-professional volunteers for such efforts in wildlife ecology and management can be a powerful tool; popularly termed citizen science, and referred to herein as participatory science, its benefits can include larger societal benefits by deepening community scientific literacy and making scientific initiatives more accessible (25). As such, I choose to use the more inclusive term 'participatory science' over 'citizen science' as the former more accurately describes the scope of public participation in and benefit from such efforts beyond those possessing government-issued proof of citizenship (26). Despite the putative benefits, researchers are increasingly concerned about the quality of training and expertise leveraged in such efforts and how they might affect the precision of estimates, particularly when participants differ significantly from scientists and technicians involved in the same efforts (25,27–30). Therefore, I hope to add to this existing corpus of literature to help inform the construction and evaluation of such programs.

Study Aims

I aim to examine the Wisconsin Department of Natural Resources' (DNR) wolf census methods to quantify: 1) Whether comparisons of wolf abundance between different periods of sampling are valid, 2) To what extent the methods used by the DNR may have led to greater uncertainty in wolf numbers than reported, and 3) To evaluate how the data under this fresh examination strengthens or weakens DNR's wolf management policy decisions. To support study aims 2 and 3, I also aim to simulate what winter wolf track results would have been if only volunteers and only DNR trackers had counted wolves across all analyzed blocks and years.

Hypotheses

In these analyses, I cannot presume to analyze how and why DNR made decisions without documentation to that effect; however it is useful to consider that DNR may have selected blocks for double surveying (survey by both volunteers and DNR in a single winter) by three alternate mechanisms: (1) at random (2) a-priori based on expected wolf density (3) based on unexpected results from the first survey.

Accordingly, I set up the following explanatory hypotheses should I detect a measurable difference between how volunteers and DNR trackers count wolves, versus a null hypothesis that they count wolves the same: (1) Volunteers count more wolves than DNR because they are more enthusiastic and may either put more effort into counting wolves or unconsciously misidentify coyote/dog tracks as wolves as a result (**Amateur Enthusiasm Hypothesis)** (2) DNR count more wolves than Volunteers because they are more skilled at finding and identifying wolf tracks (**Technical Skill Hypothesis)** (3) One tracker type counts more wolves than the other because they double survey blocks where the previous count was oddly low **(Verification/Belief Hypothesis)** (4) One tracker type counts wolves differently because they counted in different periods when wolves aggregate early in winter and disaggregate later in winter **(Ecological Hypothesis)**

I note that, for the ecological hypothesis, I do not speculate whether disaggregation or disaggregation would lead to greater counts by trackers; disaggregation may lead to greater probability of encounter in a given area, but lower probability of detection and aggregation may lead to greater probability of detection but lower probability of encounter.

The self-scrutiny conducted and presented by the DNR around 2003 suggests that the Technical Skill Hypothesis may have contributed to the discrepancies they detected (18). A 2018 DNR presentation states that only volunteers with no experience detected measurably fewer wolves than DNR trackers, and in fact volunteers with more than 80 hours of experience detected more wolves than DNR trackers; the latter discrepancy is presented as DNR trackers spending less effort when surveying the same blocks as experience volunteers. The time period and statistical methods applied for this analysis were unspecified, but the contents of the presentation suggest that, following the 2003 report, the DNR was confident in the quality of data from all but the most novice of volunteer trackers (31).

Methods

I. Survey Blocks

I only retained survey blocks that were surveyed for all wolf-years in the study period, that is from winter 2003-2004 till 2010-2011 (8 total census periods, hereafter referred to as 2003-11). As detailed below, I did receive GIS files for survey blocks as of 2020, however, for the years in question, I had to rely on the figures provided in the DNR wolf reports. With consideration for the resolution of the figures provided, I decided whether survey blocks changed in any significant way between any of the census years. I censored blocks from analysis according to the following rules: (1) If a block changed in size/coverage, that did not necessarily remove it from analysis, as I retained year specific spatial information on each block; however, because I saw it necessary to include a spatial autocorrelation correction factor in my analyses, I decided to remove blocks if their adjacency to other blocks changed between any of my survey years; to retain maximum data, I removed the fewest number of blocks to retain adjacency (that is, if either removing both blocks 5 and 7 would remove adjacency issues, or just block 3, I would remove block 3) (2) If DNR split a single block into two blocks or merged two blocks into a single block, I removed them from analysis; while conceivably I could have retained them as an artificial single block throughout analysis, the changing nature of trackers made this impossible (that is, if block 20 split into 20A and 20B, and in 2004-2005 DNR tracked wolves in 20A and volunteers tracked them in 20B, combining the blocks would mix levels of the parameter of interest into a single data point). (3) I tested the inclusion of a conditional autoregressive (CAR) spatial autocorrelation correction; this precluded inclusion of any blocks that lacked neighbors, and so for analyses including CAR autocorrelation corrections, I removed survey blocks 132 and 133 from analysis. I ended up with 124 retained for my analyses (Figure 2)

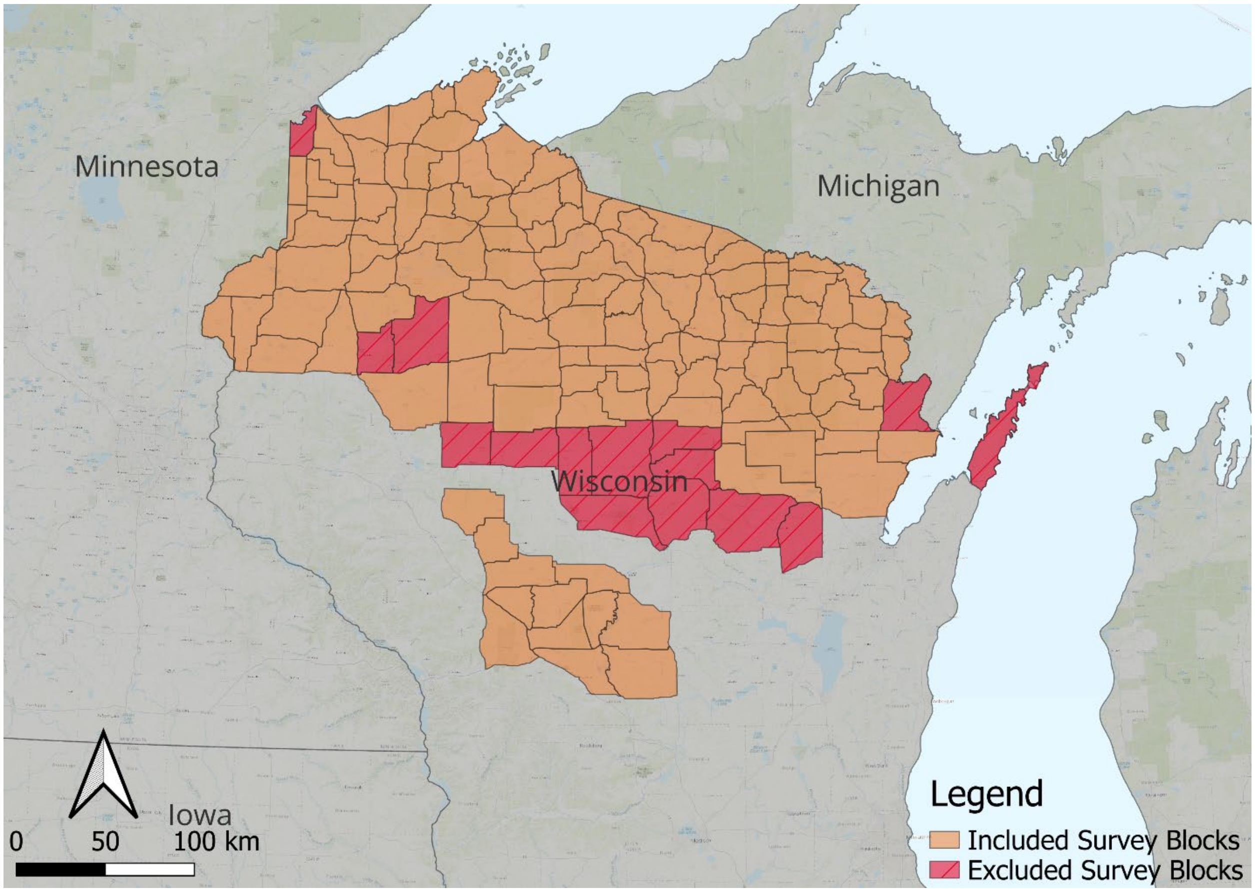


Figure 2: Survey Blocks included in final statistical analyses used by Wisconsin DNR trackers and trained volunteers for winter wolf track surveys from 2003 to 2011. Survey blocks shown reflect survey block extent and shape in winter 2010-11.

DNR provided GIS shape files for the survey blocks via email correspondence in 2020 [Shannon McNamara, email correspondence]; however, upon visual inspection, the border of the GIS survey blocks sometimes differed significantly from the figures provided in DNR population reports for the years analyzed. As such, I edited survey blocks within QGIS v3.34.14 with GRASS v 7.12. See Appendix 1, section A for a detailed list of methods and survey block edits made.

II. **Wolf Count Uncertainties**

I treated WI DNR Wolf reported uncertainty by multiple imputation of reported ranges, where if a tracker reported an estimate of wolf counts between X and Y wolves in a given block, I used multiple imputed data sets drawing from a uniform distribution of integer wolf numbers between X and Y. I tested for asymptotic model results when deciding on the number of imputed data sets. I detail further treatment of reported uncertainty in Appendix 1, section B.

III. **Model Parameters and Priors**

I detail model parameters and priors in Table 1 along with sources. I used weakly or noninformative priors as conservatively as possible. Where I used weakly informative priors, the parameter estimates did not differ appreciably from using uninformative default priors, but did improve computational performance.

To incorporate spatial autocorrelation, I decided that first order spatial autocorrelation by adjacency was most relevant, where a wolf pack may be double counted in adjacent survey blocks, as acknowledged in DNR Wolf Population Reports (32). Given polygon tolerance issues, in QGIS, I used a 5 km “buffer” to force adjacent blocks to ‘overlap’ and I derived my adjacency matrix from the resultant overlaps. I chose 5 km as it generated the appropriate overlap between adjacent blocks (based on DNR reports) without introducing ‘new’ adjacencies.

IV. **Statistical Analysis**

I analyzed the data using linear mixed effects models with wolf count as the response variable and with survey block identity as a random intercept effect. Since the data was count data with a high number of zero values, I considered default, zero-inflated and hurdle versions of Poisson and negative binomial distributions to model the error on the response variable.

I completed statistical analysis with R package 'brms' in R version 4.3.1 via the University of Wisconsin-Madison's Center for High Throughput Computing (33). I chose a Bayesian package because 'brms' allowed more flexibility for autocorrelational structure specification than other popular and well documented packages like 'nlme'. Bayesian methods of reporting parameter estimates also avoid some of the concerns surrounding usage of p-values in frequentist settings, allowing for a more robust discussion around how much support a given estimate might have (22,34,35).

Table 1: Variable definitions and priors for Bayesian mixed effects model investigating the effect of tracker identity on Wisconsin winter wolf surveys, 2003-11.

Variable	Definition	Prior	Justification
Tracker	Volunteer or DNR	$\sim N(0,1)$	Uninformative prior because this is the parameter of interest
Miles Driven	Miles driven by the trackers, Z-scaled	$\sim N(.5,1)$	Weakly positive, under the assumption that survey effort correlates to wolves found or wolves expected
Summed wolf suitability	2009 wolf habitat suitability indices calculated by Mladenoff et al(36), summed across all cells in a survey block, Z-scaled	$\sim N(.5,1)$	Weakly positive prior, assuming that large, suitable blocks are more likely to contain more wolves
Mean wolf suitability	Mean survey block value of 2009 wolf habitat suitability indices calculated by Mladenoff et al(36)	$\sim N(.5,1)$	Weakly positive prior, assuming that more suitable blocks are more likely to contain more wolves
Area	Area of the survey block in square kilometers, Z-scaled	$\sim N(.5,1)$	Weakly positive prior, assuming that large blocks are more likely to contain more wolves

Road Density	Density of roads (km roads/km^2 area) in a survey block using 2009 data from the Wisconsin Department of Transportation, Z-scaled	$\sim N(0,1)$	Uninformative prior, as road density may correlate either to increased ability to do surveys, or to decreased habitat suitability
Year	Ordinal year of the study (e.g. winter 2003-04 corresponds to 1, etc.)	$\sim N(.5,1)$	Weakly positive prior, given a generally growing wolf population
Cull	Percent of year with liberalized wolf culling per Chapron and Treves 2016 (37)	$\sim N(-.5,1)$	Weakly negative, assuming that liberalized culling reduces wolf populations
Double-surveyed	If block was surveyed by both Volunteers and DNR in the same winter, or just one tracker	$\sim N(0,1)$	Uninformative prior, no assumptions made about the nature of double surveying a survey block

Model Selection

I used stepwise backwards elimination to select variables; starting with a fully specified model, I eliminated the least suggestive variable based on degree of overlap of the 95% credible interval of the variable's posterior estimate with 0. I also generated models by testing alternate removal of variables that I expected to covary strongly, starting with the fully specified model. I did this because the complexity of the model prevented the use of a formal test for covariance using a variance inflation factor (VIF). I then used LOO (Leave-one-out cross-validation) and WAIC (Widely Available Information Criterion) for model comparison and selection.

Because 'brms' does not generate these metrics for the final imputed model, but rather for the first imputed model, I instead compared all imputed models. That is, if I ran two models with 3 imputed datasets each, I compared the evaluative criteria across all 6 individual models to make a judgement on the weight of evidence for one model over another.

Imputed Set Convergence

To determine a sufficient number of imputed datasets, I compared coefficient estimates for single imputed dataset models, 2 imputed dataset models and 3 imputed dataset models.

Runtime parameters

Model complexity required model-by-model adjustments to iteration and warmup count to achieve convergence with low R-hat and sufficient ESSs. I started all models with 4 chains and 2000 iterations (1000 warmup), an adapt_delta of 0.9 and a maximum tree depth of 20. I ended up running my final model for 16000 iterations to achieve convergence and reliable posterior estimates.

Simulations

After choosing my final model, I simulated wolf counts across all analyzed blocks and years as if both volunteer and DNR trackers had surveyed every block in every year. I retained reported counts, and used multiple imputation with a uniform distribution to account for uncertainty in reported counts. When one tracker did not survey a block, I considered two simple simulation strategies: 1) I adjusted the existing count from one tracker to the other using the marginal effect of tracker identity from the final model, thus assuming that all other covariates remain the same, and 2) I adjusted simulated wolf counts by first adjusting miles driven by tracker type, then adjusting wolf count by marginal change in miles driven, then adjusting wolf count by tracker identity. I ran 1000 simulations per year.

To test whether adjusting miles driven was reasonable given the data, I ran a paired Wilcoxon Rank Sum test on miles driven by volunteer and DNR trackers in double surveyed blocks; if I found that volunteer and DNR trackers differed in miles driven at an alpha of .05, I then considered it reasonable to conduct a simulation with miles adjusted by ‘missing’ tracker.

Results

I. Number of Imputed Datasets

Below I describe how I determine the number of imputed datasets I used to generate my final model. I refer to a given model or dataset as an n-imputed model or dataset where n refers to the number of included datasets that informed the model.

I generated 10 different imputed datasets using randomly chosen seeds. I tested models for coefficient convergence for models with one, two, and three imputed datasets, randomly chosen; I compared all 10 possible 1-imputed models, and 5 randomly generated sets of 2 and 3 datasets each. While 1-imputed dataset models and 2-imputed dataset models sometimes diverged from each other, I found that 3-imputed dataset models always produced convergent model estimates, so I completed all final comparisons and conclusions with models built on 3 imputed datasets. Using more imputed datasets did not improve model estimates or uncertainty and were computationally taxing, hence my choice to remain at 3-imputed models.

II. Model Selection

I used Leave-One-Out Cross Validation (LOO) and Widely Available Information Criterion (WAIC) to assess model fit and parsimony. The top performing models and their model fit criteria are summarized in Table 2 (I also included the difference in expected log predicted density (ELPD_diff), which shows the difference between a given model's predictive accuracy and the top performing model's predictive accuracy). The top performing model across all metrics was Model 7.

Table 2: Top performing Bayesian mixed effects models and model fit criteria for wolf counts during winter track surveys in Wisconsin, 2003-11. Results are shown for first imputed sub-model for each model (each model contains 3 imputed sub-models), but results are similar across imputed sub-models.

Model	Model Parameters	LOOIC	ELPD_diff	WAIC
7	$Log(Wolves) \sim \beta_0 + \beta_1 Miles + \beta_2 Tracker + \beta_3 Yr + \beta_5 MeanProb + \beta_6 Area + \beta_7 Density + \beta_8 Both + \beta_9 Cull + (1\|SB) + AR(1) + \epsilon$	5441.0	0.0	5389.4
1	$Log(Wolves) \sim \beta_0 + \beta_1 Miles + \beta_2 Tracker + \beta_3 Yr + \beta_4 SumProb + \beta_5 MeanProb + \beta_6 Area + \beta_7 Density + \beta_8 Both + \beta_9 Cull + (1\|SB) + AR(1) + \epsilon$	5441.6	-0.3	5390.6
8	$Log(Wolves) \sim \beta_0 + \beta_1 Miles + \beta_2 Tracker + \beta_3 Yr + \beta_4 SumProb + \beta_7 Density + \beta_8 Both + \beta_9 Cull + (1\|SB) + AR(1) + \epsilon$	5443.9	-1.5	5392.6
2	$Log(Wolves) \sim \beta_0 + \beta_1 Miles + \beta_2 Tracker + \beta_3 Yr + \beta_4 SumProb + \beta_5 MeanProb + \beta_6 Area + \beta_7 Density + \beta_9 Cull + (1\|SB) + AR(1) + \epsilon$	5449.8	-4.4	5400.1

I chose a hurdle negative binomial response for superior model performance, owing to explicit considerations for zero-inflated count data with overdispersion at higher values (38). I checked for well-mixed chains and high overlap in the posterior predictive plot to confirm model convergence and strong model performance (Appendix 1, Figure A2-A3).

III. Model Results

Fixed effect estimates with 95% credible intervals for one of the three submodels from Model 7 are shown in Table 3. These are shown as incidence rate ratio (IRR) estimates rather than raw coefficient estimates, since a (hurdle) negative binomial model's coefficients are otherwise proportional to the exponentiated variables. Incidence rate ratios are multiplicative, so an IRR below 1 and above 1 are indicative of negative and positive effects on the response variable respectively, while an IRR of 1 indicates no discernible effect on the response variable. For the total model, the posterior estimate for volunteer IRR is 0.83 (95% CI: [0.74-0.92]). This indicates that, all else being equal, volunteers counted on average 83 percent as many wolves as DNR trackers. This credible interval is highly suggestive of a difference between volunteer trackers and DNR trackers, especially given that Bayesian orthodoxy (based on stability) tends to prefer an 89% credible interval (39). Miles driven, year, survey block area, and mean suitability were all positively correlated with wolves counted with a 95% credible interval entirely above an IRR of 1. Being double surveyed was strongly suggestive of a lower wolf count, with an IRR of 0.87 (95% CI: [0.79, 0.95]), indicating that double surveying may occur when wolf counts are low. While liberalized killing and road density were retained in the final model, their weakly negative effects were not strongly indicative of an IRR below 1.

Table 3: Fixed Effect predictor estimates (transformed to Incidence Rate Ratios) on wolves counted during Wisconsin winter track surveys (hurdle negative binomial model) 2003-11. Results are shown for 1 of 3 imputed submodels, other submodels show similar results.

	Wolves Counted	
Predictors	*Incidence Rate Ratios*	*CI (95%)*
Intercept	1.27	0.57 – 2.53
Miles Driven (Z-Scaled)	1.17	1.13 – 1.21
Tracker [Volunteer]	0.83	0.74 – 0.92
Year	1.07	1.04 – 1.09
Area of Survey Block (Z-scaled)	1.16	1.05 – 1.29
Mean Wolf Suitability	3.64	1.92 – 6.92
Percent of Year with liberalized wolf killing	0.98	0.87 – 1.11
Double-Surveyed	0.87	0.79 – 0.95
Road Density (Z-scaled)	0.94	0.84 – 1.05
N_{SB}	124	
Observations	1191	

IV. **Simulated Wolf Counts**

Prior to simulating wolf counts, I tested whether DNR and volunteer trackers differed significantly in miles driven per survey block. I found that DNR trackers did drive significantly fewer miles per survey block than volunteer trackers using a paired Wilcoxon signed-rank test ($p<0.05$). Given uncertainty in how survey effort was adjusted between tracker identities, I simulated wolf counts across all survey blocks by tracker type both with (Figure 3) and without (Figure 4) adjusting miles driven. I discuss the uncertainty in adjusting miles in the discussion. More details on the simulations can be found in Appendix 1, section D.

Figure 3: Simulated wolf counts by tracker identity, without adjusting miles driven Wisconsin, 2003-11. Points are median simulated counts, shaded regions are 95% confidence intervals. Wolf counts were simulated for all survey blocks included in the Bayesian mixed effect model.

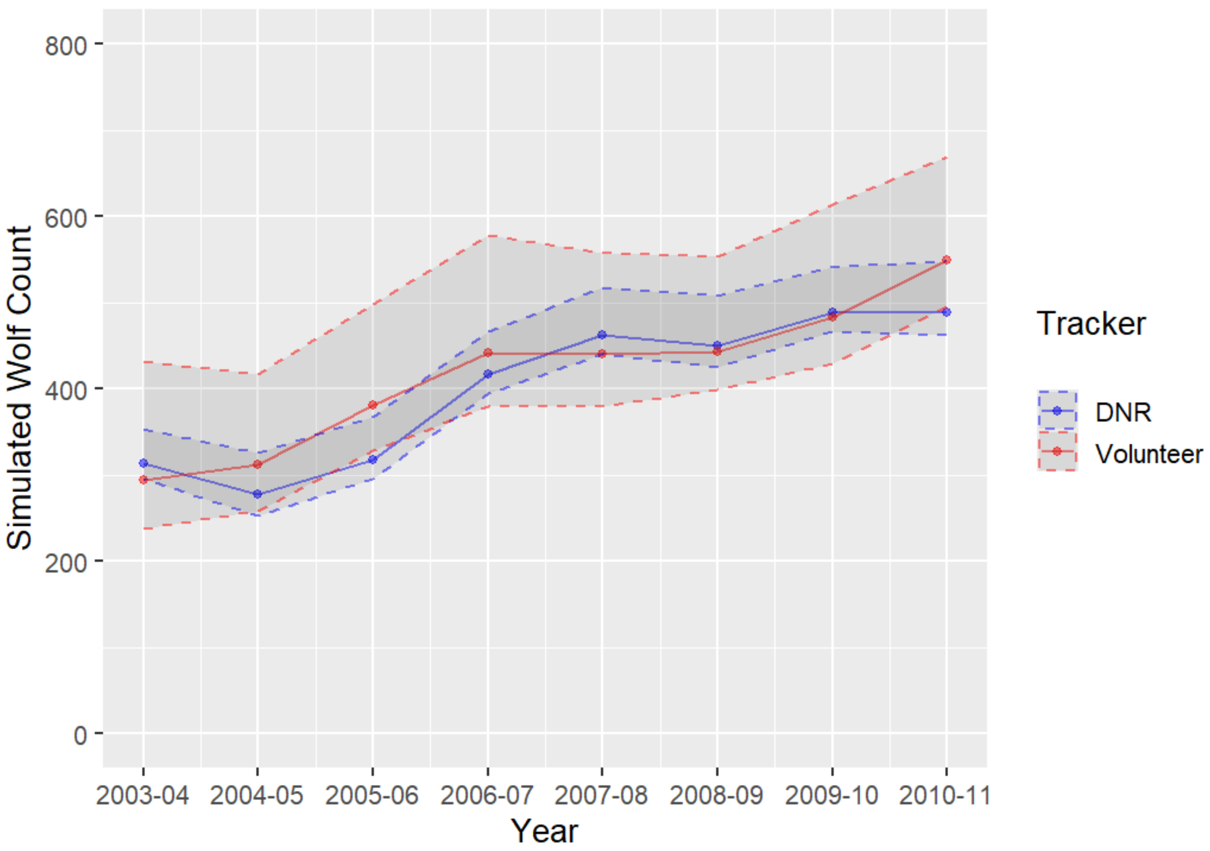


Figure 4: Simulated wolf counts by tracker identity including adjustment of miles driven, Wisconsin, 2003-11. Points are median simulated counts, shaded regions are 95% confidence intervals. Wolf counts were simulated for all survey blocks included in the Bayesian mixed effect model.

Without adjusting miles driven, Figure 3 shows volunteers simulated as consistently counting fewer wolves than DNR trackers with no overlap in the 95% confidence intervals. The difference in median simulated wolves counted varies between a low of 28 in 2004-05 to high of 134 in 2010-11. Considering the lower bounds of the volunteer simulation and the upper bounds of the DNR simulation, the plausible discrepancy in simulated wolf counts in 2010-11 is as much as 154 wolves.

When adjusting miles driven, the simulations in Figure 4 show much larger confidence intervals for simulated wolf count, and consequently show overlap and intersection between DNR simulated wolf counts and volunteer simulated wolf counts. Neither tracker identity counts consistently higher or lower total wolves. The larger confidence intervals produce a wide range of plausible wolf counts, with a plausible range of as little as 158 wolves in 2004-05 and as much as 216 wolves in 2005-06.

Discussion

I found that volunteers counted wolves differently than DNR trackers during annual wolf track surveys in Wisconsin during the period encompassing winters 2003-04 to 2010-11. Specifically, all other measured variables being equal, volunteers on average counted 83% [95% CI: 0.74-0.92] the number of wolves that a DNR tracker would in the same survey block. I use a 95% credible interval because 1) it is more conservative than the Bayesian orthodoxy of an 89% credible interval and 2) for the superficial ease of comparing it to the oft-used frequentist 95% confidence interval (39).

As a result, I reject the null hypothesis that volunteers and DNR trackers on average count the same number of wolves in the same survey block, all other variables held equal. Likewise, I reject the Amateur Enthusiast hypothesis, which stated that volunteers may on average count more wolves than DNR trackers because they put either greater energy into counting wolves or unconsciously misidentify other canid tracks as wolves. This leaves the technical skill hypothesis (DNR counted more wolves than volunteers because DNR trackers are more skilled at finding, identifying, and discriminating wolf tracks), the verification/belief hypothesis (DNR counted more wolves than volunteers because they double count blocks where they believed the volunteer count was too low) and the ecological hypothesis (DNR counted more wolves than volunteers because they counted wolves during periods of the year when wolf detection was easier than the periods during which volunteers counted wolves).

Without data on the timing of individual surveys, it is impossible to falsify or verify the ecological hypothesis. I would suspect that the small number of DNR trackers (59 reported for 2018-19, unclear for other years) would make it very difficult for the DNR trackers to complete their surveys during a relatively discrete period in winter (31). I would also imagine that volunteers would complete their surveys largely as their personal and professional lives allowed. Nevertheless, we cannot reject this hypothesis.

The technical skill hypothesis, if correct, suggests that volunteer training remained insufficient despite improvements made in 2000-2003 (17). If so, it may remain insufficient today.

The Verification/Belief hypothesis suggests opposed alternate mechanisms. It may be that DNR trackers truly found more wolf tracks when following-up on volunteer tracker counts that they believed were undercounts through greater search effort, this would dovetail somewhat with the technical skill hypothesis. Alternately it may be that, upon expecting that there should be more wolves in an area, DNR trackers purposefully or subconsciously inflated wolf counts upon their recount of the survey block. If correct, our study identifies one grassroots mechanism whereby an agency may create a political population, unintentionally or intentionally (10). I note that double-counting a survey block had a strongly suggestive negative correlation with wolf count, where double counted blocks had roughly 87% (95% CI: [0.79, 0.95]) the number of wolves as single-surveyed blocks, all else being equal, lending some support to the possibility that DNR trackers may have followed up where they perceived volunteer wolf counts as low. However, as I detail below, the documentation behind how DNR survey effort was related to double-surveying makes this inference less clear.

The simulations in Figures 3 and 4 bear further discussion. At first glance, it would seem that adjusting for miles driven corrects for a systematic difference in how volunteers and DNR count wolves. However, it is unclear how and when DNR trackers drive fewer miles. In my miles-adjusted simulation, I simulated the number of miles driven by each tracker type based on the ratio of volunteer to DNR miles driven in co-surveyed blocks. However, a 2018 presentation by the DNR indicated that when DNR trackers co-survey blocks with experienced volunteer trackers, they may intentionally reduce survey effort (31). Therefore, adjusting simulated DNR wolf counts down and simulated volunteer wolf counts up based on hypothesized reductions and increases in respective survey effort may be an overcorrection for survey blocks with inexperienced volunteers. It is likely that the 'true' discrepancy in total wolf counts by year would lie somewhere between Figures 3 and 4.

However, what Figures 3 and 4 do give us are rough estimates of uncertainty for the winter wolf counts. The simulated counts (unadjusted for miles driven) vary by up to 154 wolves in 2010-11 when the upper and lower bounds of the volunteer and DNR 95% confidence intervals are taken into account. Adjusting for miles driven, the larger confidence intervals show that in the same year, winter wolf counts may plausibly vary by up to 198 wolves. By comparison, the DNR reported a maximum discrepancy of 56 wolves between DNR and volunteer trackers in 2010-11, where both tracker types surveyed 86 blocks each, and the final aggregated wolf estimate (including additional information sources like howl surveys and radio collared wolves) was given with an uncertainty of 42 wolves (40). It is obvious that simulating counts for both tracker types across a subset of survey blocks is not directly comparable to reported numbers from all survey blocks, or to an aggregate wolf population number that incorporates several data types. However, this comparison serves to illustrate how non-transparency in censusing technique makes replication of Wisconsin's wolf estimates during this period impossible, and how unaccounted for biases in the methods may have led to an underestimate of uncertainty in wolf population estimates. Overdispersion in population counts can have profound effects on wildlife management, as managers may overestimate population growth and consequently overestimate population viability, as has been argued for tigers in Asia (13,41).

The skeptical reader may feel such old data are irrelevant to current management. However, the winter tracking program has continued to the present day, with 16009 miles of track surveys completed in 2023-24, 3462 by volunteers (42). Moreover, the state has adopted a new scaled-occupancy model for estimating gray wolf populations, with substantial input from the winter track surveys (21,43); as such, the potential for systematic biases between DNR and volunteer trackers is as important now as it was in 2011, especially given the state's population-specific wolf management strategy as of the 2023 wolf management plan (16,43).

There are several resultant implications for management.

Firstly, it should follow why, when census periods differ substantively in their methodologies, then their results should not be combined into a single time-series uncritically (44). The introduction of two significantly different methods (DNR and volunteer trackers) represents two substantially different estimates of abundance (Table 3) (Figures 3-4) which cannot be combined without explicit accounting for these discrepancies in the statistical analysis. This suggests multiple potential solutions.

One solution would be to split population analyses by periods of methodological consistency. Solely looking at usage of volunteer trackers to aid in winter wolf tracking counts, such analyses should be split at minimum into 5 periods: (1) 1979-1994 when volunteers were used informally and sparingly (2) 1994-2003 when the program was formalized (and even herein, volunteer usage expanded between years) (3) 2003-2011, the period I have analyzed, after the update in volunteer training and supervision (4) 2012-2019 after significant turnover in the composition of volunteer trackers in response to state wolf policy changes (volunteer letter here) and (5) 2020 to present, after the adoption of the scaling occupancy method (17). The fourth and fifth change were roughly coincident with sudden reductions in the transparency of reporting on the winter wolf tracking results, making a similar analysis of the period post-2011 impossible independent of the DNR (45).

However, I recognize that demanding the strenuous partition of data may be impractical from a practical management perspective. Given that the DNR should have access to more detailed and more extensive data than I had access to in this analysis, they may seek to conduct and publish a detailed analysis such as the one conducted here. Such an analysis may be instructive of a simple statistical correction to prior wolf population estimates, or of a simulation to assess uncertainty in point-estimates more rigorously. Among other data, the DNR should have detailed information on volunteer experience and how DNR trackers decided on their block-by-block survey effort, which would add greater clarity both to regression analysis and count simulations than I was able to achieve. This could allow more rigorous and transparent wolf population estimates even across changes in methodology.

Connected to the above, I suggest that the Wisconsin DNR may seek to investigate procedural causes of the difference between DNR and volunteer trackers that I found. Such a difference suggests that volunteer training may require renewed scrutiny (Technical Skill Hypothesis). Alternatively, if instead the issue lies in the timing of tracking surveys relative to wolf aggregation (Ecological Hypothesis), then I suggest reporting the timing of surveys completed as part of the monitoring; while it would be at least partially collinear with tracker identity in this case, it would lend greater transparency to the census and analysis.

A common theme of my suggestions is the need for greater transparency in how Wisconsin DNR reports methods and results of wolf population monitoring. I applaud the detailed reporting that allowed my analysis of this period, but it is discouraging that such information is no longer readily accessible starting with the 2012-13 wolf population report (46). Furthermore, my analyses were limited even within this period by incomplete data reporting and an unclear method for aggregating data into a final wolf population estimate. If Wisconsin intends to claim a scientific approach to wolf monitoring and management, then independent scientists should be able to replicate and potentially critique how Wisconsin counts wolves.

Chapter 2

Fear in the Taiga: Nonlethal effects of Amur tigers on their ungulate prey in the Russian Far East

Introduction

Ecologists in the 21st century have been increasingly interested in top-down trophic influences on ecosystem function and regulation, as a complement to bottom-up effects of primary producers and abiotic resources. Top-down effects take special importance for an increasingly threatened global clade of large carnivores, who often function as the top predators in their given ecosystems. Large carnivores have been lost at accelerated rates in the 20th and 21st centuries relative to many other mammalian clades, owing to life history characteristics and human actions that bring them into conflict and competition with humans (1,47–49). It is therefore critical to understand the top-down influences that large carnivores exert on their ecosystems both for a scientific understanding of ecosystem structure and dynamics, and as support for the global conservation initiatives aimed at preventing extinction of large carnivores.

The direct effects of large carnivores and other top predators on their prey can be separated into two categories: 1] lethal effects (LE) and 2) nonlethal effects [NLE]. Lethal effects are exerted through the direct killing predators do, reducing overall densities or specific demographic stages of one or more prey species (50). Nonlethal effects are popularly referred to as the 'ecology of fear' or more recently the 'landscape of fear', where cues of predator presence or vulnerability to attack can induce behavioral changes in the prey animal (51–53). This behavioral effect can manifest in physiological changes due to stress, differential use of the landscape, and trade-offs between foraging and antipredator behaviors (50,54–57)

I note here that while much of the prevailing literature distinguishes between consumptive and nonconsumptive effects, I am instead focusing on lethality as the causal mechanism as Lima 1998 did (58); I argue that whether or not the predator consumes whatever it has killed, the demographic or behavioral effects on the survivors remain, and moreover this broader terminology allows for extension of such dynamics to killing motivated by competition (interspecific predatory conflict) in addition to killing motivated by consumption (50,54,59).

Top predators are hypothesized to cause a trophic cascade, where their lethal or nonlethal effects on their prey species are so strong that the trophic levels below said prey species are also affected, and thus the effects of the predator are felt throughout the ecosystem. Large carnivores are often specialized to prey upon mammalian herbivores, so the hypothesized and realized effects of large carnivore induced trophic cascades are often reflected in altered vegetation structure and density (48,49,53,60–63).

Tigers (*Panthera tigris*) are top terrestrial predators in every habitat they occupy throughout South and East Asia, if one ignores the role of humans (64). Therefore, many studies and conservation initiatives have touted the tiger's disproportionate ecological influence; this has partially motivated tiger conservation efforts (65,66). However, to my knowledge, this claim has never been rigorously tested. The hypothesized trophic cascade caused by tigers would be expressed in either LE or NLE on their prey, and in this study I investigated a narrow set of potential NLE mechanisms.

Among large carnivores, nonlethal effects have most famously been studied in gray wolves, both in Yellowstone National Park, where these effects are disputed, and in Wisconsin (61,62,67–69). However, ecological theory predicts that coursing predators such as wolves exert fear effects on prey differently than would ambush predators like tigers. Arthropod systems reveal some experimental evidence for these between coursing and ambush predators. Two potential mechanisms underly this proposed difference. The first is that the distance between attack site and kill site is generally much greater for coursing predators, changing the selective potential for risk cues at the attack site. If a prey animal is chased over several kilometers by a coursing predator before being killed, then we may expect that the features of the attack microsite and the kill microsite differ depending on the route taken by the prey. Survivors may escape predation by either mechanism of avoiding attack or by eluding pursuit, producing complex, differential selective pressures on prey populations modulated by both attack and kill site. The second mechanism theoretically differentiating NLE exerted on prey between coursing and ambush predators is that the advantage gained by prey species by using vigilant antipredator behaviors is much higher when dealing with an ambush predator that relies on a close, stealthy approach for predatory success versus a coursing predator that may launch a successful attack even if detected on approach (50,54,70–73).

Vigilance as an antipredator behavior merits further scrutiny. Head-up visual scanning behavior may support functions beyond predator detection and avoidance, including resource search, intraspecific interaction, and locomotion (74). Two assumptions underpin the interpretation of vigilance as an important antipredator behavior: 1) Vigilant individuals are superior at detecting predators compared to nonvigilant individuals and 2) Early predator detection increases the probability of preventing or escaping predatory attack (70,72). Some studies of vigilant behavior in birds have questioned the validity of these assumptions. Lima and Bednekoff 1999 demonstrated that even birds in a 'non-vigilant' head-down posture detected a simulated predatory attack, albeit more slowly than birds in a 'vigilant' posture, and Tatte et al 2019 found that more vigilant birds were slower to detect and escape a simulated predator than nonvigilant birds (72,75). Therefore, assumptions about head-up postures may be overly simplistic. However, field studies on several ungulate prey species still suggest that 1) cues of predatory risk induce head-up vigilance in prey and 2) vigilant individuals are less likely to succumb to predatory attack than nonvigilant individuals (55,56,76–82).

I also tested for the effects of tiger predation risk cues on ungulate visit duration and grouping patterns. Lima 1992 proposed that when a predator is sufficiently deadly and difficult to detect it is more advantageous for prey to reduce attack exposure rather than increasing vigilance (70). Wikenros et al 2014 found support for this hypothesis with deer species reducing visit duration but not increasing vigilance when exposed to olfactory cues of lynx (*Lynx lynx*) (77). The relationships between grouping patterns, predation risk and vigilance are complex without a clear pattern across the available literature (74,83). Larger groups with greater intragroup cohesion may be more conspicuous on the landscape, but they may also be better able to defend themselves and better able to detect potential predators than an individual or a disaggregated group (74). Further, individuals may benefit from dilution of risk per attack launched when they are in a large, cohesive group (74). Experimental literature remains unresolved on how group size relates to anti-predator vigilance and whether social cohesion increases in response to perceived predation risk, but it remains an important aspect of predator-prey study (74,83–85).

Therefore, I cautiously retain vigilance, defined functionally in my methods, visit duration, and grouping behavior as antipredator behaviors of interest, tested against the manipulated conditions that I describe hereafter. I also analyze foraging behavior to test whether responses to predatory risk cues are associated with reduced foraging.

Here I report experimental tests aimed at manipulating the ‘fear’ effect on ungulate prey exposed to a variety of cues of tiger presence and vulnerability to attack. I conducted these experiments in Sikhote-Alin Biosphere Zapovednik (SABZ), a protected area in the Russian Far East with a well-studied population of Amur tigers. While this subpopulation is no longer defined as a distinct subspecies, it remains genetically distinct and spatially separated from other mainland tigers (86,87). Although prey density for experimentation is much lower in this region than in other areas of tiger distribution, the clade of overlapping carnivores in Central Primorye is also relatively smaller than in other areas of South and East Asia (64,88). Leopards, dhole, and wild dog species are not found in SABZ, removing a confounding variable (89). For example, interspecific competitors may have similar dietary niches to tigers, and as such, modeling those putative landscapes of fear as single-predator systems may be oversimplifications (64,90–97). Recent review papers have highlighted this conceptual deficiency in much of the predator-prey literature (98,99).

By contrast, SABZ has relatively few sympatric predators that course and stalk large ungulate prey. Lynx, brown bear, red fox, golden eagles, and various mustelid species are sympatric with the Amur tiger in SABZ. During the winter, when brown bears hibernate, the other sympatric carnivores are far less likely than tigers to prey upon adult ungulates, particularly red deer and wild boar, because of their size and defensive ability (88,100). Therefore, tigers in SABZ provide a test of NLE effects on wild prey with fewer confounding effects of other predators and an area little visited by human hunters.

I set up camera stations in a part of SABZ located by the coast with the Sea of Japan to study how ungulate prey, primarily red deer (*Cervus canadensis*), wild boar (*Sus scrofa*) and sika deer (*Cervus nippon*) would react to cues of tiger presence. Between three field seasons, with variations in experimental setup explained in the methods, I tested the NLE of three potential cues of recent tiger presence: (i) Olfactory (tiger feces versus a presumed non-predatory control mesopredator feces) (ii) Auditory (periodic playing of long distance advertisement calls of tigers versus presumed non-predatory control mesopredator calls) (iii) Visual (obscured vision during head-down foraging behavior versus an unobstructed control in which head-down individuals could still potentially detect an approaching predator).

In Poland, Kuiper et al found that fresh wolf scats provoked a significant increase in vigilance behavior in red deer versus a control, whereas Wikenros et al found that lynx scat provoked a decrease in site visitation time for roe deer and red deer (77,101). Fresh fecal accumulation may be an effective indicator of a nearby tiger because tigers may spend up to several days in a single area, particularly while consuming a large prey item (102,103). Kerley et al studied tiger diet composition via scat analysis at three separate sites including SABZ, indicating that tiger scat does persist in the environment, rather than being swiftly removed by scavengers or decomposition (104); my own field experiences indicate that large carnivore scat in the area may persist for several days. I tested the olfactory cues throughout all field seasons.

Both Schaller 1967 and Yudakov and Nikolaev 1987 observed fear behavior in potential tiger prey which was possibly explained by olfactory cues of tiger presence. Schaller observed a herd of seven chital deer (*Axis axis*) retreat from an area after having visibly sniffed the air, and upon further inspection, he noted that a tiger had been present a night earlier (105). Yudakov and Nikolaev, after long-term observations of Amur tigers in the region of my fieldwork, describe wild boar, roe deer (*Capreolus capreolus*) and brown bear (*Ursus arctos*) individuals variously retreating from recent tiger dens and tiger tracks, though whether the fear stimulus in each case was visual or olfactory was not clear (103). Therefore, I hypothesized that olfactory cues of tiger presence, simulated here by the placement of tiger feces, would induce antipredator behaviors in ungulate prey.

Petrunenko et al 2016 analyzed habitat correlates of prey vulnerability in Amur tiger range, and among them, found that landscape 'openness' correlated negatively with tiger kill-site selection (65). These results suggest that the inverse of landscape openness, vegetation density, would be positively correlated with tiger kill-site selection. In studies on tiger predation on livestock in India, Miller et al 2015 similarly found that tiger kill sites were strongly associated with dense forest areas (106). I therefore hypothesized denser vegetation provides cover for tigers to more easily approach prey undetected, and to therefore launch a successful attack. I sought to simulate this in my experimental setup by baiting my sites and comparing two conditions for foraging, one where the foraging animal's vision is impeded by a an obscuring fabric material, and an opposed condition where the animal's vision is unimpeded. This had the additional experimental benefit of enhancing the potential fitness cost of head-down foraging, potentially increasing effect size. This follows the work by Lima and Bednekoff as well as Tatte, indicating that nonvigilant animals with unobscured line-of-sight may still be capable of detecting and escaping attack (72,75).

In 2020 and 2021 I added an auditory risk cue in an attempt to compensate for reduced sample size. I detail the circumstances around these changes in the methods. There is a robust literature on the effects of predator playback on prey, including response to tiger vocalizations. Although most predators do not vocalize while hunting, many prey species nevertheless display antipredator behaviors in response to predator playback (107). Among reported prey responses to predator playbacks are displays of vigilance, alarm calls, reduced foraging, and initiation of flight away from the source of the sound (78,85,107–111). Most of these experiments involved either (i) direct playback to observed prey species and immediate recording of their responses or (ii) regular habitat-scale playback over an extended period of days to weeks, with behaviors recorded within period (107,112,113). In contrast, I played calls once a week in a brief pulse during site visitation. I intended for these auditory treatments to enhance the effect size of my olfactory cues, so I matched the auditory and olfactory treatments at each site.

In sum I implemented three conditions (odor cues, auditory cues, and obstructive cover) to understand their impact on antipredator behaviors (vigilance, foraging, visit duration, and group aggregation) to test hypotheses of NLE on Amur tiger prey.

Methods

Location

I worked in Sikhote-Alin Biosphere Zapovednik (SABZ), a highly protected area in the center of Amur tiger habitat located by the town of Terney on the Sea of Japan (Figure 1).

Experimental Setup

I conducted 25 weeks of experiments over the course of three field seasons: 2019 [April-July], 2020 [January-March] and 2021-22 [October-January]; I had to suspend work in March 2020 due to the COVID-19 pandemic and returned in Fall 2021 to finish the experiments I had begun. Hereafter I refer to these as the 2019, 2020, and 2021 seasons respectively. The 2019 season differed substantially from the subsequent two seasons, due to the onset of African swine fever (ASF) in the region (Table 1) (114). Zapovednik officials prohibited the continued use of supplemental food bait during these seasons to prevent increasing aggregation of wild boar and potentially accelerating the progression of ASF. I substituted introducing food bait with artificial scent deer lures during these seasons. I also removed the treatment wherein I obscured line of site at my bait stations, because 1) in the 2019 season, this treatment led to boar destroying several of my sites 2) without food bait, I could not localize ungulates at the bait station for their vision to be obscured reliably and 3) with potential lower sample sizes, I decided to minimize artificial elements at my sites to avoid scaring away ungulates. Finally, during the 2020 and 2021 seasons I started a supplemental playback treatment, matching the identity of the scent treatment, in a further effort to overcome lower sample size with greater effect size.

I set up all sites in the southeastern section of SABZ because of the high abundance of ungulate prey. Local colleagues with the Wildlife Conservation Society (WCS) helped me choose the exact sites (Figure 1) for experimental sites with an eye towards ungulate usage. My second criterion was ease of accessibility, as it would have been much more difficult to maintain and access the same number of sites weekly had I put them in more remote areas of the park. In choosing such areas, it is possible that results were affected by 1) abundant ungulate food resources that made the cost of antipredator behaviors less costly than in food-scarce areas and 2) the human shield hypothesis whereby human activity may create refugia for prey species from potential predators (115). I detected tiger scat and pugmarks within my study area throughout all study periods, and the reserve reported photographs of two males and one female in 2021 and 2022, therefore I reject the human shield hypothesis in this case (89); moreover, the real presence of tigers at my sites helps guard against acclimatization to perceived tiger cues that I added.

Table 1: Camera station manipulations by season for experiments testing the nonlethal effects on Amur tigers on ungulate antipredator behaviors in Sikhote Alin Biosphere Zapovednik, Russia, 2019-22.

Season	**2019**	**2020**	**2021**
Odor Cue	Yes	Yes	Yes
Food Bait	Yes	No	No
Odor Bait	No	Yes	Yes
Obstructive Cover	Yes	No	No
Auditory Cue	No	Yes	Yes

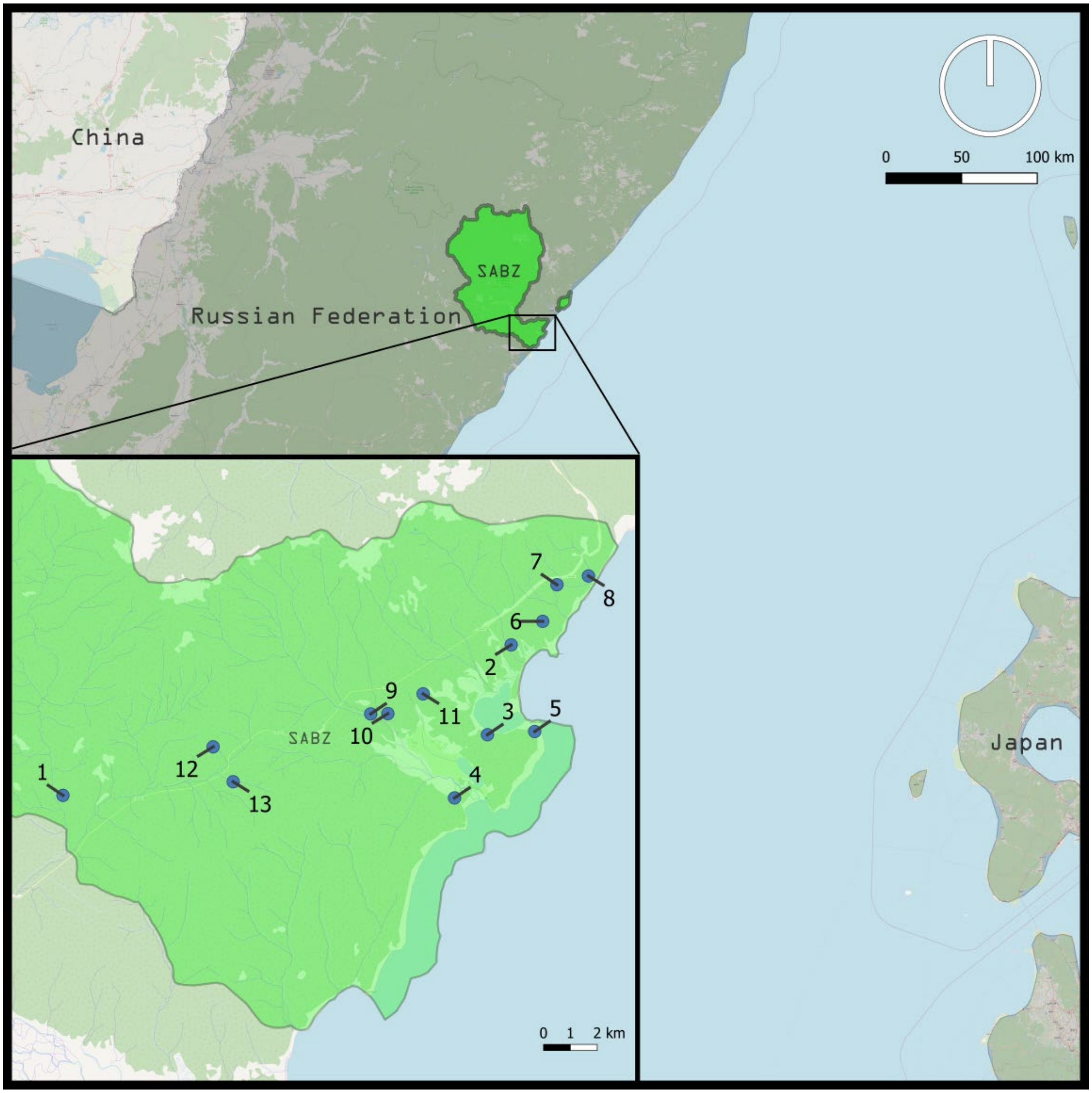


Figure 1: Location of Sikhote Alin Biosphere Zapovednik on the coast of the Russian Federation with inset showing the locations of experimental sites (numbered blue dots) for testing the nonlethal effects of Amur tigers on ungulate prey, 2019-22.

I set up sites with the scent or food baited stations by a large tree near ungulate-worn paths. I set up my main camera approximately 10 meters away from the bait station, both facing the bait station and facing away from the sun’s path. I placed the camera 180 cm above the ground to prevent deer from obscuring the space between the camera and the bait station, and I angled the camera down to cover as much of the area surrounding the bait station as possible. During the 2019 season and the beginning of the 2020 season, I also set up a camera immediately in front of the bait station, hoping to catch the feeding animal’s posture with higher clarity. However, I found that animals that ended up close to this camera were too close to clearly evaluate their posture, and so I did not use this data and eventually repurposed those cameras to expand the number of sites instead.

I hung the olfactory cue in a plastic basket with several holes at a height ~180 cm above the ground. This made it feasible to replace the olfactory cue but also to prevent wild boar from disturbing or eating the scent cue, as they did in a similar previous experiment (101). I made the fence for the bait stations and for hanging the obscuring fabric 127 cm high, to account for the size of boar skulls. Although I stopped using the obscuring fabric after the 2019 season, I kept the fence and sticks of the bait stations to hang the deer scent lures on and maintain relative similarity with the previous season. See Figure 2 for a representative diagram of site setup across seasons.

All experimental protocols were approved by the University of Wisconsin-Madison Independent Institutional Animal Care and Use Committee (IACUC: L006160-A01).

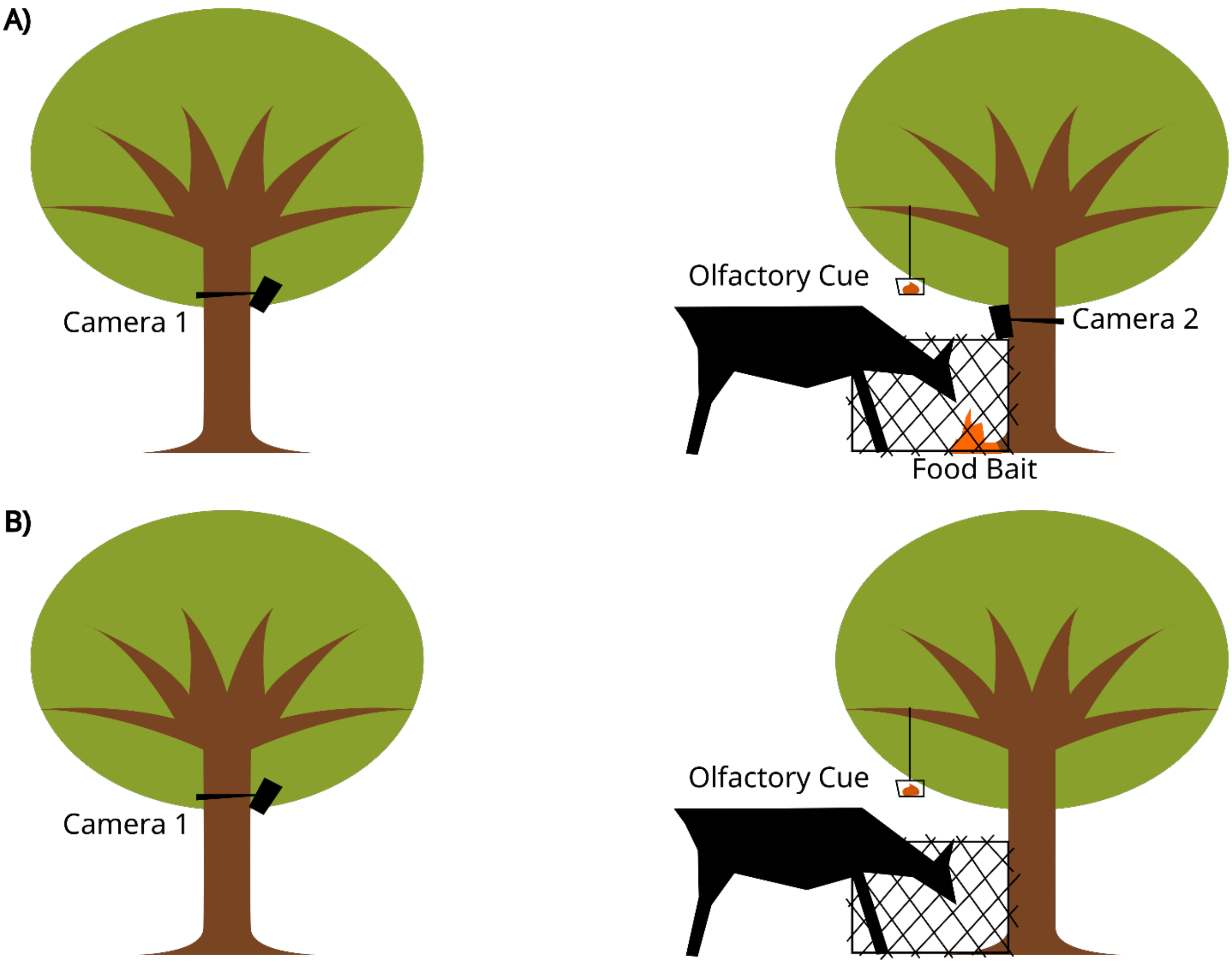


Figure 2: Experimental setup for testing nonlethal effects of olfactory cues of Amur on ungulate prey in Sikhote Alin Biosphere Zapovednik, Russia, 2019-22. A) 2019 setup when food bait was permitted and when I used two cameras per site; food bait was placed within a partially fenced area at the base of a tree B) 2020-22 setup when food bait was prohibited due to an African swine fever outbreak. Not pictured are deer urine scent cues and gathered leaf litter and loose grass added during 2020-22.

Shift in Methods

I ceased both supplemental food baiting and artificially obscuring stations after 2019. I was prohibited from supplemental food baiting during the 2020 and 2021 seasons due to concerns about African swine fever described above. I abandoned the inclusion of obscuring fabric in those seasons for several reasons. Without food bait, individual ungulates had no reason to forage within the fenced area where their vision could be obscured. I also found in 2019 that wild boar tended to eat the obscuring fabric, leading to the destruction of the site setup. Finally, the obscuring fabric would move wildly in windy conditions, which seemed to alarm ungulates; anticipating smaller sample sizes without food baiting already, I was wary of reducing that sample even further by inadvertently scaring ungulates away.

In an attempt to draw ungulates to the center of my sites without supplemental food baiting, I gathered leaf litter and loose grasses surrounding each site and placed them within the fenced area, hoping to localize visitation to where the camera trap would detect it.

After baiting was prohibited, I knew that my sample size of ungulate visitations was likely to drop significantly. To try to compensate for this loss in statistical power, I added a new auditory treatment in the 2020 and 2021 seasons, looking to potentially increase the effect size in this set of preliminary experiments on tiger NLE. Berger 2007 played back tiger calls (90-100 dB at 1 m distance) when in direct observation of red deer herds and detected significant vigilant responses versus a control sound (78). In contrast, I played tiger calls (and control mesopredator [*Vulpes vulpes*] calls) at 103-105 dB at 1 m distance during site visits to simulate latent tiger presence, but not necessarily an agonistic tiger immediately in the area during visitation (103,105). The decibel level I used roughly approximates that used in other studies, and one report measured tiger long distance advertisement calls at 80 dB 10 meters from the source (based on logarithmic scaling, my calls would be roughly 80 dB 16 meters from the source) (116).

Much of the prevailing literature on predator playback experiments has involved either (i) direct playback to observed prey species and immediate recording of their responses or (ii) regular habitat-scale playback over an extended period of days to weeks with behaviors recorded within period (107,112,113). This contrasts with my treatment where I played predator and control calls for a brief (~90s) pulse when no prey species were directly observed with inter-playback intervals of approximately one week. Moreover, where the duration of mammalian prey responses to pulsed predator playback has been reported, prey responses persist on the order of minutes, rather than days (85,117). While the literature led me to believe that my implementation of playback would be unlikely to have an effect, I nevertheless saw it as a workable last-ditch attempt at enhancing the simulation of ‘recent’ general tiger presence at my sites under changing field conditions.

Treatment and Control Conditions

I obtained animal feces from Sadgorod Zoopark in Vladivostok, Russia. Zoo staff members froze the feces in plastic bags daily and I transported them to Terney and froze them again to retain as much ‘freshness’ as possible. The zoo had badger feces for me in 2019 and fox feces in subsequent seasons for my mesopredator control. There were three tigers at the zoo during my field seasons, all of whom I obtained scat from. I obtained three tiger and two fox call sequences from the Animal Sound Archive maintained by the Berlin Natural History Museum, the Cornell Lab of Ornithology’s Macaulay Library, and from Youtube. In selecting call sequences, I sought sequences with as few background noises as possible and I removed background bird calls and human narration from the audio files. I used multiple examples for each species to guard against the possibility that an individual recording is perceived as threatening rather than that species in general. Exact catalog numbers/URLs for the calls are located in Appendix 2 (Table A1). I played each call so that the peak dB level was 103-105 dB 1 meter from the source (Turtlebox® Bluetooth Speaker Gen 1).

During the 2019 field season, I used two attractive food baits, soy and a salt block. I added 1 kg of soy to every site every time I visited (as it was wholly consumed in the interim), while I only replaced the salt block if it was effectively consumed/destroyed. I placed the food bait at the center of the fenced area, under the olfactory cue that I hung above. I always added less tiger scat (by weight) than mesopredator scat to avoid a response purely on the magnitude of the scent rather than the nature of it.

I did not begin treatments in any area until I saw ungulate visitation at that site; in that way, I sought to acclimatize ungulates to the setup and to minimize noise in the data from ungulate reaction to the novelty of the installation, rather than to my treatments.

Sequence of Treatments

Developing the methods in the 2019 pilot season I implemented treatments in a somewhat disordered manner as I learnt feasibility, while in the 2020 and 2021 seasons I implemented a more formal crossover design to account for site-specific characteristics. I randomized the initial treatment at all sites during those seasons and then alternated treatments within a site thereafter. Crossover designs use within-subject (in this case, within-site) comparisons so inter-site differences in risk, vegetation etc. would not confound comparison of treatment and control conditions.

I matched the treatment order of sites 9 and 10 due to their proximity to each other, to avoid effect-spillover between sites. I lengthened the duration of treatment and control periods from 1 to 3 weeks starting in the 2020 season, again because of the reduced sample size of ungulate visitations per period. I implemented washout periods between treatment periods to reduce the possible latent effect of one condition on the subsequent one. I used a washout period of 1-week during all seasons. Because I had to leave my 2020 season early, I treated the intervening period as a very extended washout period of over 1 year before continuing alternating treatments in 2021.

I replaced olfactory cues once per week, including during 3-week periods within each condition. During the 2020 and 2021 seasons, I played calls of tigers and mesopredators (fox [*Vulpes vulpes*]) for 90 seconds during my visits at approx. 105 decibels at 1-meter from the speaker. On testing with field partners, the sound attenuation was highly variable depending on the wind and proximity to waterways, not extending beyond 200 meters from the source.

I set up cameras to record bursts of 3-5 photos (3 photos in 2019, 5 in 2020-22) upon trigger.

Figure 3 below shows the sequence of treatment conditions across all seasons and all sites.

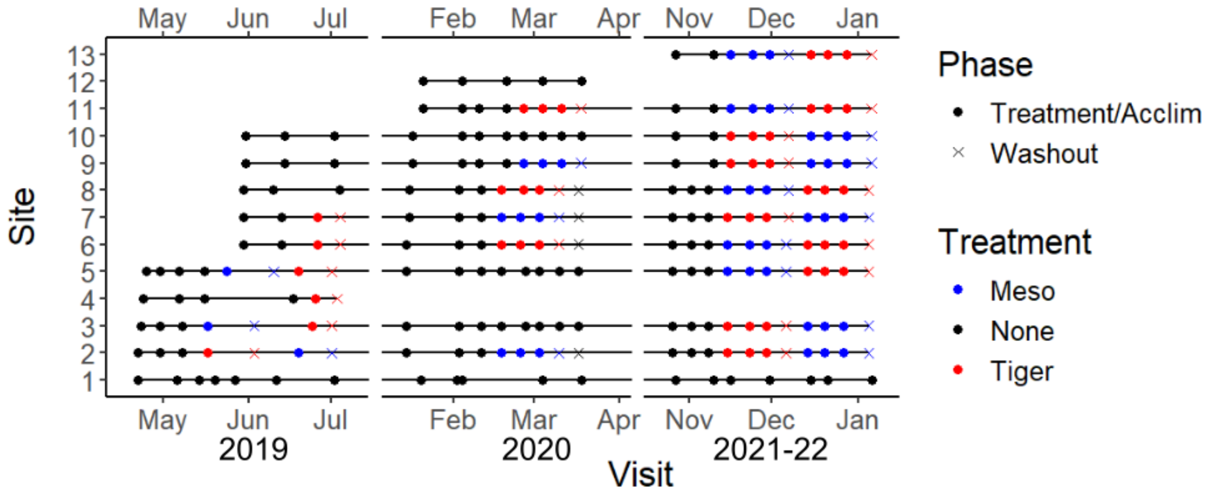


Figure 3: Order of treatments for experiments on nonlethal effects of Amur tigers on ungulate prey in Sikhote Alin Biosphere Zapovednik, Russia, 2019-22. Acclim=acclimatization period, Meso=mesopredator (control) treatment. Red (tiger) and blue (mesopredator) dots indicate a day when I added the corresponding treatment to a site up until an ‘x’, indicating the cessation of treatments and the start of a washout period. Black dots indicate acclimatization, where I visited sites but added no treatments because ungulate visitation rates were too low.

Independent visits

I treated a single visit by a single species as my unit of study. While previous similar experiments have used a 5-minute interval between successive photos/videos as the threshold for a new visit without explicit justification, I determined my interval by inspecting that photocapture patterns for each species (77,101,118). I determined the interval threshold for considering two or more photos as separate visits by creating histograms of photocapture interval for each species (between 30 seconds and 30 minutes, having decided a priori that photos within 30 seconds of each other were likely the 'same' visit and photos more than 30 minutes apart were likely separate visits). I inspected the histograms for gaps where the interval between successive photos seemed to cease incrementing continuously, and I used this criterion to decide on a threshold for considering two photos as constituting separate visits.

I did not consider intervening visitation by one species as necessarily ending the visit of the preceding species unless the 'interrupting' species was a large or medium carnivore (tiger, bear, or lynx). Mixed ungulate assemblages have been repeatedly observed in SABZ, so I did not see a compelling reason to assume that the arrival of one ungulate species would drive away another(119–121).

There is an inherent trade-off depending on the interval chosen. If I choose too short of an interval and erroneously classify one visit as several, then I risk pseudo-replication, and if I choose too long of an interval and erroneously classify several visits as a single visit, then I risk reducing the power of my analysis. Without comprehensive camera coverage of the surrounding forest or unambiguously marked animals, it is impossible to confirm the truth. Therefore, I have chosen my method to attempt to reduce pseudo-replication without losing too much power.

I tested visit duration by minutes and number of photos during the visit as predictors for analyzing the effect of treatment on vigilance. I also analyzed visit duration as a response variable.

Posture Classification

I analyzed photos for ungulate behaviors and visitation characteristics. I assigned postures to behaviors under broad umbrellas of potential antipredator utility. I restricted analysis to adults and subadults, excluding juveniles based on apparent body size and juvenile-specific pelage characteristics. I initially employed many undergraduate assistants, which I used as a first screening for species identifications, but given concerns about interobserver variability, especially with respect to more ambiguous postures (between vigilant and foraging) and to wild boar; wild boar have much stouter and less flexible necks, with heads much closer to the ground in locomotive and vigilant postures, compared to the observed deer species, so the distinction between head up and head down posture is less clear than with cervids. I classified all postures myself, after I had forgotten the order of treatments (to blind myself). Because independent visits were my unit of study, I aggregated behavior by visit.

I focused primarily on two behavior classifications: (i) Vigilant: an animal whose head is at or above shoulder height, eyes open, line of vision extending beyond an immediate substrate/conspecific, not moving rapidly (74,83) and (ii) Foraging: an animal whose head is below shoulder level, inclined towards grass/understory/bait. Foraging by this definition may include an animal moving slowly with its head held in that posture. My definition of vigilance reflects a multifunctional looking definition following Treves 2000 (74). Because wild boar are stocky, possess shorter necks than cervids, and may have naturally hunched over backs even in a head-neutral position, I used a more specific distinction to avoid ambiguity, where I only classified a boar as head-down foraging if its snout was close to the ground and inclined towards it. Figure 4 below shows examples of vigilant and foraging postures for sika deer and wild boar.

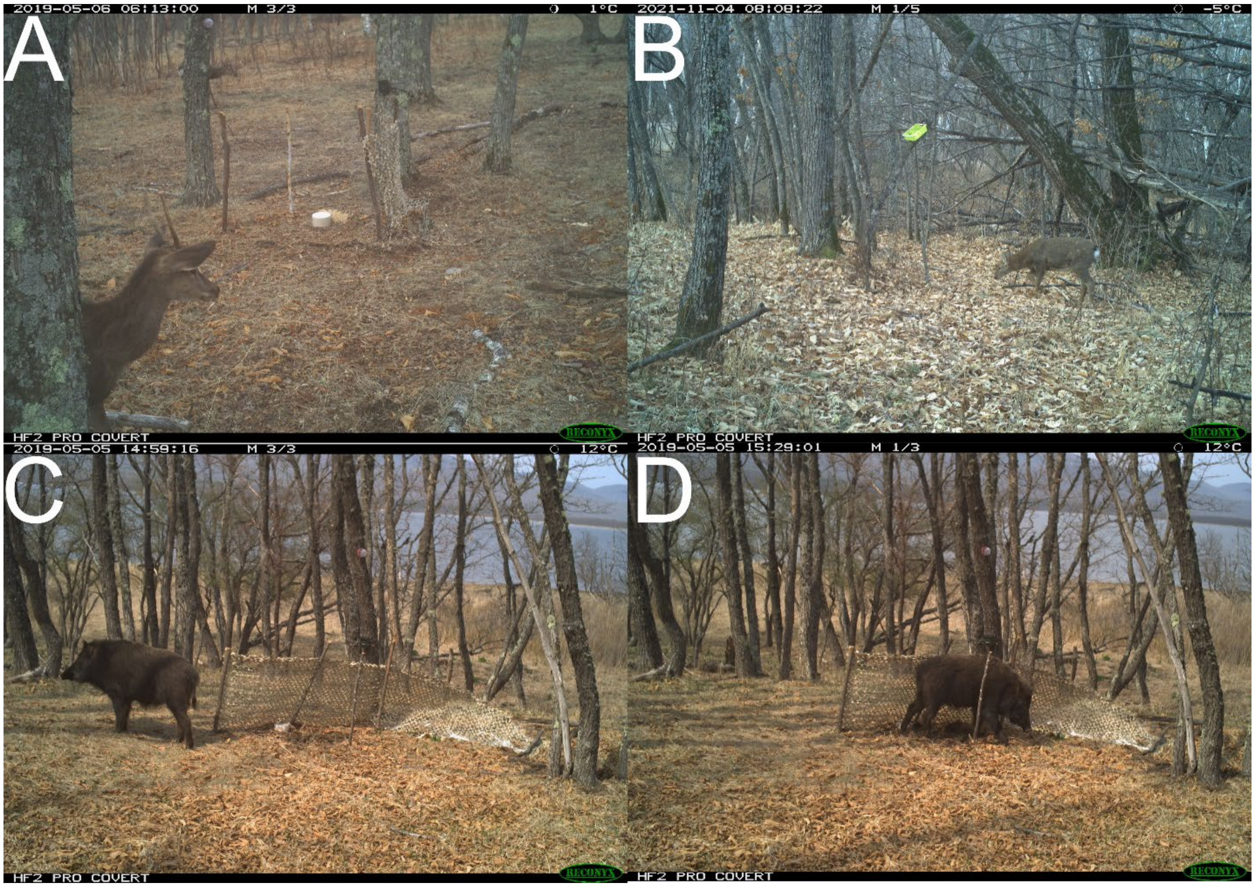


Figure 4: Examples of vigilant and foraging postures in ungulate photographs. A) Vigilant sika deer (*Cervus nippon*) B) Foraging sika deer C) Vigilant wild boar (*Sus scrofa*) D) Foraging wild boar. Red deer (*Cervus canadensis*) postures are analogous to those of sika deer.

I did not analyze behaviors outside of vigilance and foraging, as the sample size and distribution among treatments of these behaviors was insufficient for analysis. However, I also recorded escape behaviors (rapid acceleration/change of direction initiated in-frame, confirmed by two or more photos) as an antipredator behavior, and affiliative, self-grooming, and resting (animal is seated/laying down and non-vigilant) as non-defensive behaviors. Finally, I also recorded two sets of behaviors that were ambiguous with respect to antipredator utility: (i) investigative postures (posture where an animal is directly interacting with the bait station materials such as the fence or the obscuring fabric) and (ii) transit (rapid movement initiated outside of the frame). I classified animals with an entirely unclear posture as unknown.

I classified all subadults and adults within range of the camera; I noted other individuals in the background for group size metrics, but I did not include their postures because they would not have provided independent samples of behavior, and they may have been too far from the olfactory cues to perceive them. I classified all party members within range of the camera rather than picking a random individual because it would be impossible to tell whether scent is being picked up in one direction or another by the wind and to retain maximum information on ungulate behavior. By restricting my estimates of party size to individuals visible in frame, this is always an underestimate of true party size.

I retained the maximum number of animals captured in one photo (excluding background individuals) as a group aggregation parameter hereafter referred to as maximum clumping.

Analysis

I intended to analyze my more careful crossover design implemented in 2020 and 2021 with the Hills-Armitage approach as detailed by Diaz-Uriarte (122). However, likely due to the cessation of food baiting, as well as the drop in wild boar densities due to African swine fever, my sample size in 2020 and 2021 dropped significantly from 2019, so that data during the treatment and control periods of those seasons was sparse and intermittent (123). Due to small sample sizes, I was unable to retain categorical month as a variable, therefore I was unable to account for period effects finer than season during analyses. Therefore, I instead used mixed-effects models, and I aggregated data across all three field seasons. I separated analyses by prey species. I only retained visits during experimental 'Tiger' treatment periods or control 'Mesopredator' treatment periods, discarding visits from the acclimatization and washout periods.

I tested four potential antipredator response variables in my analyses: total vigilance behaviors recorded across all individuals during a visit, total foraging behaviors recorded across all individuals during a visit, total visit duration (minutes), and maximum clumping. To preliminarily check the effect of changing methods after 2019, I conducted simple Wilcoxon Rank-Sum tests to compare response variables in 2019 to response variables in 2020 and 2021 grouped together. I used a significance threshold of .05 for these tests. Given a significant difference, I would run analyses for the ungulate in question separately for 2019 visits and for 2020 and 2021 visits grouped together.

Table 2 summarizes all tested predictors for each response variable. I included a two-factor treatment parameter (tiger or mesopredator) for olfactory/auditory treatment. I also included a two-factor parameter (present or absent) for the inclusion of the obscuring fabric treatment; this value was 'absent' for all of 2020 and 2021. I retained a three-factor 'season' variable (2019, 2020, 2021) as well as an interaction term for treatment and season to account for both coarse temporal effects and the change in methods that occurred between 2019 and 2020. I treated site as a random effect in all models to account for site-specific characteristics. I included variables for carryover effects from directly preceding treatments (none, tiger, or mesopredator). I also included time of day as a two-factor parameter (day or night), determined by whether the photograph was in color (day) or infrared (night). For some analyses, I included the number of adults and subadults (hereafter referred to as number of adults for concision), number of juveniles, number of photos taken, and duration of visit in minutes. Because the number of photos and visit duration are naturally collinear, I tested these predictors in separate models rather than including them together. I discuss these predictors in greater detail below. I never photographed red deer fawns, so I did not include number of juveniles in any red deer models. I also did not get any red deer visits with the obscuring fabric installed at the same time as an experimental tiger treatment or control mesopredator treatment was implemented, so I did not include this variable in red deer models.

Table 2: Predictors tested against antipredator response variables for mixed effects models analyzing the nonlethal effects on Amur tigers on ungulate antipredator behaviors in Sikhote Alin Biosphere Zapovednik, Russia 2019-2022.

Predictor	Definition	Tested against?			
		Visit Duration	Maximum Clumping	Vigilance	Foraging
Treatment	Sensory cue: Tiger, Mesopredator	Yes	Yes	Yes	Yes
Time of Day	Day, Night	Yes	Yes	Yes	Yes
Obscuring Fabric	Present, Absent	Yes	Yes	Yes	Yes
Season	Field Season: 2019, 2020, 2021	Yes	Yes	Yes	Yes
Season*Treatment	Interaction term of Season and Treatment	Yes	Yes	Yes	Yes
Carryover	Carryover effect from preceding treatment: Tiger, Mesopredator, None	Yes	Yes	Yes	Yes
Number of Adults + Subadults	Highest number of adults and subadults seen in one frame, including background individuals	Yes	No	Yes	Yes
Number of Juveniles	Highest number of juveniles seen in one	Yes	No	Yes	Yes

	frame, including background individuals				
Duration	Length of visit in minutes	No	Yes	Yes	Yes
Number of photos	Number of photos taken during the visit	No	Yes	Yes	Yes
Site	Random effect of site	Yes	Yes	Yes	Yes

I needed to distinguish instances of high vigilance due to lengthy visits or large numbers of adults from high vigilance due to experimental manipulation. Therefore, I tested the inclusion of visit duration, number of photos, and number of adults as predictors in analyzing vigilance. However, given that I hypothesized potential effects of the treatment on visit duration (highly collinear with number of photos) and maximum clumping (highly collinear with number of adults), I run the risk of decreasing test power in analyzing vigilance. Therefore, I ran mixed effects models on duration and maximum clumping prior to analyses of vigilance to detect a potential confounding effect. The same concerns are true for analyses with foraging as a response variable of interest, which I likewise analyzed after analyses of visit duration and maximum clumping.

I considered that vigilance may respond nonlinearly to visit duration (duration in minutes, or number of photos) or group size (number of adults) (70,74,76,124–126). Prior to running mixed effects models on vigilance, I compared vigilant behaviors against number of adults, number of photos, and visit duration respectively, and compared linear and nonlinear (square root, squared, and log) simple regressions. Using corrected AIC (AICc), I determined whether it was reasonable to test a nonlinear relationship between vigilance and duration, number of photos, or group size.

I used backwards selection and AICc for multi-model comparison. In models where I tested between number of photos and visit duration as measures of the length of a visit, I ran backwards selection separately on models with each of these measures. I started all models with the maximum number of predictors, and I tested for multicollinearity with GVIFs. I removed the variables with the largest GVIF values until all variables showed a GVIF below 2.5; where GVIF values were similar (within 1) I retained the parameter of greater interest, for example I would retain the Treatment parameter rather than the Carryover parameter in such a case. After removing variables using GVIF, I removed variables by highest p-value until either coming to a model with all fixed effects at a p-value below .05, or until the model became entirely uninformative (e.g. a single fixed effect). I then compared all models using corrected AIC (AICc) and chose the model without multicollinearity with the lowest AICc score.

I conducted all analyses in R version 4.4.0 using package coin (for Wilcoxon Rank Sum tests) and package lme4 for mixed effects analysis. In addition to the default gaussian specification, I tested a Poisson regression specification for maximum clumping, since group size is a form of count data.

Because I am conducting a novel experiment and conducting multiple tests, I chose to use a more conservative alpha value of 0.001 as my threshold of significance as prescribed by Colquhoun (35). For any results above an alpha of 0.001 but below the more conventional alpha of 0.05, I will be more conservative about my interpretation of the coefficient's significance. For results above an alpha of 0.05 and below 0.1, I will discuss potential implications in the context of a weakly suggestive effect.

Results

Independent visit threshold

I considered visits from the same species to be independent when there was a 20-minute or larger intercapture interval for wild boar and when there was a 10-minute or larger intercapture interval for red deer and sika deer. I decided on these thresholds using histograms of intercapture interval for each species (See Appendix 2 Figures A1-A3). The data on red deer was much sparser than the other two species, therefore I chose 10 minutes to be conservative and to match with sika deer, rather than a shorter interval such as 7.5 minutes. Using those thresholds, I ended up with 46 independent visits of red deer (across 883 photographs), 178 independent visits of sika deer (across 5437 photographs) and 282 independent visits of wild boar (across 9447 photographs). However, when restricted to only visits during tiger and mesopredator treatments, the sample size drops further to 96 independent wild boar visits, 61 independent sika deer visits, and 8 independent red deer visits. Figure 5 shows the distribution of this final sample size of visits by season and species.

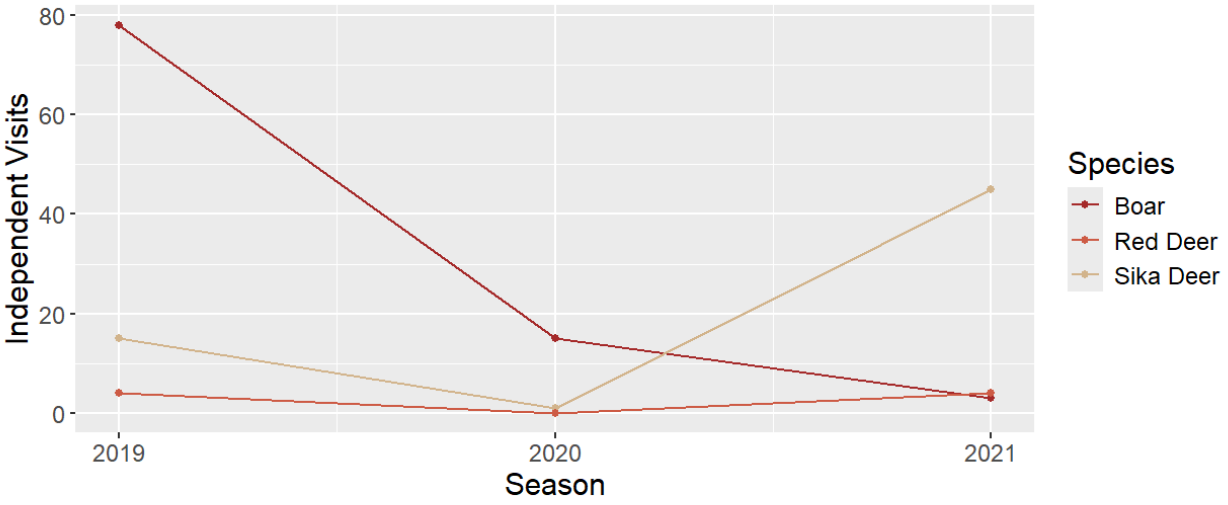


Figure 5: Distribution of ungulate visits to experimental across field seasons sites in Sikhote Alin Biosphere Zapovednik, Russia. Independent visits designated by an intercapture interval of 10 minutes for sika deer and red deer and 20 minutes for wild boar.

Wilcoxon Rank Sum Tests for preliminary assessment of methods change

None of the antipredator response variables (vigilance, foraging, visit duration, maximum clumping) for any of the ungulates showed a significant difference at the 0.05 level between 2019 and the 2020/2021 seasons so I did not separate analyses by season.

Effect of tiger cues on antipredator behaviors

1. Site Visit Duration

Fixed effect estimates for the best supported models predicting wild boar, sika deer, and red deer site visitation duration are presented in Table 3.

The most supported wild boar indicated that presence of the obscuring fabric had a significant ($p<0.001$) positive correlation with visit duration, where wild boar tended to spend 13.32 additional minutes at sites with the obscuring fabric versus those without. 'No' carryover effect had a suggestive ($0.001<p<0.05$) positive correlation with visit duration (Table 3). There was no carryover effect only at the beginning of a field season, indicating that this predictor may be indicative of the effect of site novelty. In this case, at sites with no carryover, boar seemed to spend 7.59 additional minutes versus following a mesopredator treatment. At a much weaker suggestive significance level ($0.05<p<0.10$), tiger sensory treatment may have also been positively related to wild boar visit duration, potentially correlating to 5.57 additional minutes at a site versus the mesopredator control. The other fixed effects in the wild boar model, while improving model fit, had p-values too large ($p>0.10$) for me to make inferences on potential relationships.

The only fixed effect of note in the most supported sika deer model was the number of juveniles, which had a weakly suggestive ($0.10>p>0.05$) positive correlation with visit duration (Table 3). While the tiger sensory treatment parameter was included and showed a positive correlation with visit duration again, the coefficient estimate was too insignificant ($p>0.10$) to draw meaningful inference (Table 3).

The most supported red deer model included only one fixed effect, time of day. As with both wild boar and sika deer, the sign of this coefficient was negative, but with a p-value too large to make inferences about the system.

Table 3: Mixed linear regression coefficients for the most supported models estimating the factors affecting site visit duration for wild boar, sika deer, and red deer in Sikhote-Alin Biosphere Zapovednik 2019-22. Each column represents a separate regression model for each prey species. Intercepts and random effects of site are excluded from the output.

	Wild Boar	Sika Deer	Red Deer
Treatment [Tiger]	5.57 *	0.15	
Time of Day [Night]	-1.04	-0.06	-0.93
Obscuring Fabric [Present]	13.32 ***	-0.16	
Season [2020]	-3.30	0.97	
Season [2021]	0.47	1.88	
Carryover [None]	7.58 **		
Carryover [Tiger]	6.30		
Number of Adults + Subadults	3.13	0.30	
Number of Juveniles	0.11	3.80 *	
Num.Obs.	96	61	8
* p<0.1, ** p<0.05, ***p<0.001			

2. Grouping Behavior (Maximum Clumping)

Fixed effect estimates for the best supported models predicting wild boar and sika deer, maximum clumping behavior are presented in Table 4. Across the eight red deer visits during control and experimental treatments, a single red deer was detected five times and two red deer were detected three times; as such I discarded analysis of maximum clumping with red deer. I tested Poisson specified models in addition to the default Gaussian models, however the sika deer Poisson models failed to converge, so I used a Gaussian specification for both wild boar and sika deer for ease of comparison.

Number of photos was a highly significant (p<0.001) positive predictor for both wild boar and sika deer (Table 4). This is an intuitive result, as one might expect that the more individuals in front of the camera trap at once, the more likely the camera is to be triggered. The magnitude of this effect was low for both species (Estimated at 0.003 additional adults and subadults in frame at one time per additional photo for wild boar; Table 4 only shows 2 decimal places). The most supported sika deer model retained the sensory treatment variable, where tiger cues were weakly (p>0.10) positively related to clumping behaviors. Other retained variables like obscuring fabric presence and season were also nonsignificant (p>0.10).

Table 4: Mixed linear regression coefficients for the most supported models estimating the factors affecting maximum clumping behavior for wild boar, and sika deer in Sikhote-Alin Biosphere Zapovednik 2019-22. Each column represents a separate regression model for each prey species. Intercepts and random effects of site are excluded from the output.

	Wild Boar	Sika Deer
Number of Photos	0.00 ***	0.04 ***
Treatment [Tiger]		1.18
Obscuring Fabric [Present]		-1.33
Season [2020]		-2.08
Season [2021]		1.19
Num.Obs.	96	61
* p<0.1, ** p<0.05, ***p<0.001		

3. Vigilance

I tested whether vigilance for each species may be related to nonlinear functions of number of adults, duration of visit, and number of photos taken by way of AICc comparison prior to building mixed effect models. I found that there was support for testing a 2nd degree polynomial of duration versus wild boar vigilance, a square root of duration versus sika deer vigilance, and a 2nd degree polynomial of number of adults versus wild boar vigilance. There was some support for nonlinear relationships between predictors and red deer vigilances, however the Akaike weight in favor of a linear relationship was nontrivial in each case; combined with the small sample size ($n=8$) of red deer visits, I decided that a higher order predictor was likely overfit.

Fixed effect estimates for the best supported models predicting total vigilant behaviors for wild boar, sika deer, and red deer are presented in Table 5. None of the most supported models included nonlinear terms. Number of photos was highly significant ($p<0.001$) and positively correlated to both wild boar and sika deer vigilant behaviors, supporting the intuitive assumption that the more photos per visit, the more behaviors of any type may be observed. At a weaker level of significance ($0.05<p<0.10$), number of photos also showed a positive correlation to the number of vigilant behaviors for red deer (Table 5).

Group size appeared to have a strong positive effect on recorded vigilance for wild boar. The number of adults and subadults had a highly significant ($p<0.001$) correlation to number of vigilant behaviors, supporting another intuitive assumption that the more individuals photographed, the more behaviors of any type may be observed (Table 5). More interesting is the suggestive ($0.001<p<0.05$) positive correlation that number of juveniles had with boar vigilance (I note that juveniles did not contribute to the sample size of vigilance or other behaviors) (Table 5). For every additional juvenile, it appears that adult and subadult boar may display on average 3.73 additional vigilant behaviors. This may be suggestive of either increased vulnerability of sounders with piglets to predation, or of a social function of looking between mature boar and piglets. However, I note that there was only one wild boar visit with piglets present in my analyses, so this result may be an artifact of low sample size. The presence of the obscuring fabric had a weakly suggestive ($0.05<p<0.10$) positive correlation with wild boar vigilance, where boar may have showed 5.1 more vigilant behaviors in the presence of obscuring fabric than without. Given that wild boar were actively interacting with the obscuring fabric in photos, this may have more to do with interest in the fabric itself rather than simulating a ‘riskier’ low visibility landscape as I had intended. Sensory tiger cues had a nonsignificant ($p>0.10$) positive correlation with wild boar vigilant behaviors.

The 2021 season had a weakly significant ($0.05<p<0.10$) negative correlation with sika deer vigilance versus the baseline 2019 season. The 2020 season had a nonsignificant ($p>0.10$) negative correlation with sika deer vigilant behaviors as well, as did both 2020 and 2021 seasons for wild boar vigilance (Table 5). These may be indicative of an effect of winter, since the 2020 and 2021 seasons took place largely during winter (October-March) while the 2019 baseline season took place in spring and early summer (April-July); winter food scarcity may increase the cost of antipredator vigilance versus warmer months (127). However, these effects are too insignificant to rely on for inference.

Table 5: Mixed linear regression coefficients for the most supported models estimating the factors affecting vigilance behavior for wild boar and sika deer in Sikhote-Alin Biosphere Zapovednik 2019-22 Each column represents a separate regression model for each prey species. Intercepts and random effects of site are excluded from the output.

	Wild Boar	Sika Deer	Red Deer
Treatment [Tiger]	0.20	3.92	
Time of Day [Night]	3.59	-0.61	
Obscuring Fabric [Present]	5.10 *	6.36	
Season [2020]	-0.74	-21.27	
Season [2021]	-1.83	-15.01 *	
Number of Adults + Subadults	6.04 ***	1.32	
Number of Juveniles	3.73 **	3.33	
Number of Photos	0.34 ***	0.67 ***	0.37 *
Treatment [Tiger]:Season [2020]	8.25		
Treatment [Tiger]:Season [2021]	-0.23		
Num.Obs.	96	61	8
* p<0.1, ** p<0.05, ***p<0.001			

4. Foraging

Fixed effect estimates for the best supported models predicting total foraging behaviors for wild boar, sika deer, and red deer are presented in Table 6. As with vigilance, number of photos was highly significant ($p<0.001$) and positively correlated to both wild boar and sika deer vigilant behaviors, and suggestively significant ($0.001<p<0.05$) and positively correlated with red deer foraging, lending further support to the assumption that the more photos are captured, the more behaviors of any type may be observed (Table 6).

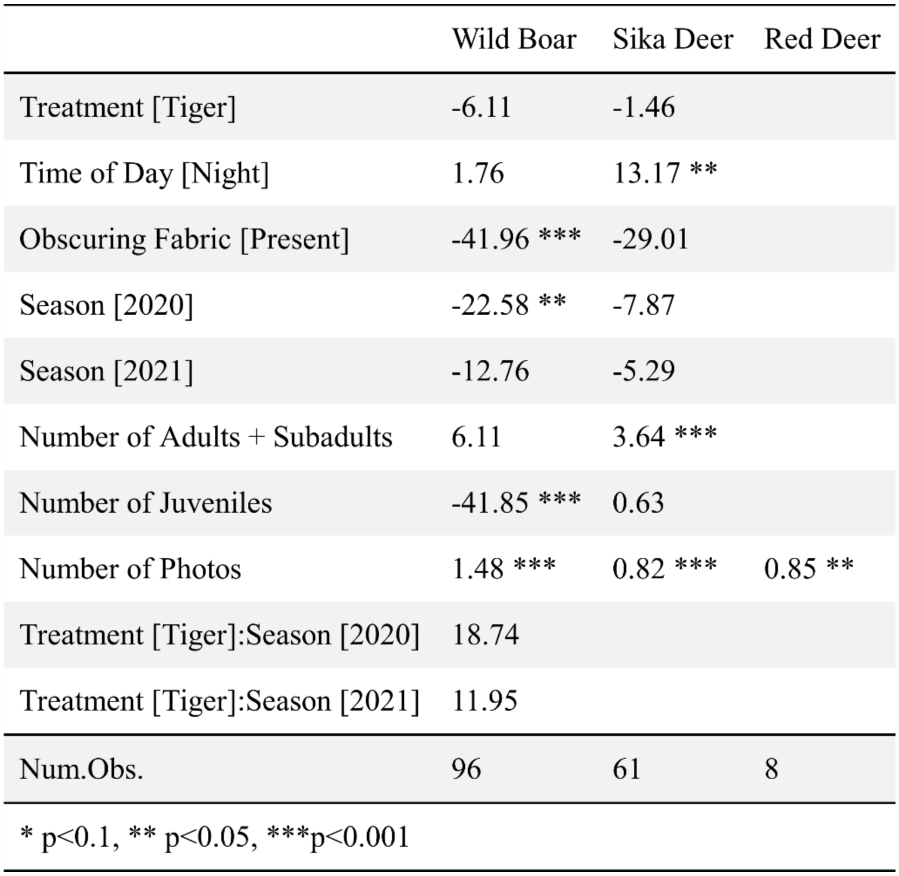
Number of juveniles and the presence of the obscuring fabric both show highly significant ($p<0.001$) negative correlations with wild boar foraging behaviors (Table 6). Presence of the obscuring fabric is associated with 41.96 fewer foraging behaviors versus no obscuring fabric. This is likely because boar spent a great deal of time interacting with the fabric (which I recorded as an 'Investigative' behavior), tearing at the fabric and seemingly attempting to consume it in lieu of vegetation. Every additional piglet was associated with 41.85 fewer foraging behaviors, indicating that the increase in mature boar vigilance associated with piglets may come at the expense of foraging; however, once more the single data point with piglets present makes me cautious about inferring too confidently from this result. The 2020 season had a weakly suggestive ($0.05<p<0.10$) negative effect on foraging versus 2019, where boar in 2020 seemed to forage 22.58 fewer times than in 2019. 2021 also had a negative correlation with wild boar foraging versus 2019, albeit non-significantly. The arrival of African Swine Fever in 2019, the change from spring to winter, and the prohibition on food baiting, make it impossible to make a clear inference on these weakly observed effects (114).

Sensory tiger cues had nonsignificant ($p>0.10$) negative correlations with foraging for both wild boar and sika deer (Table 6).

Number of adults and subadults had a highly significant ($p<0.001$) and intuitive positive effect on observed sika deer foraging behaviors in the most supported model (Table 6). Visits at night were also suggestively ($0.001<p<0.05$) positively correlated to increased foraging, where night visits may have been associated with 13.17 more foraging behaviors than daytime visits. Contrary to the expectations from the sika deer vigilance model, where I speculated that weakly observed negative effects of the winter seasons on vigilance may have been due to winter food scarcity, the nonsignificant ($p>0.10$)

effects of winter seasons on sika deer foraging are also negative. However, it should be noted that in addition to the season change, I used food bait in 2019 and ceased in 2020 and 2021, naturally decreasing the available food at sites.

Table 6: Mixed linear regression coefficients for the most supported models estimating the factors affecting foraging behavior for wild boar, and sika deer in Sikhote-Alin Biosphere Zapovednik 2019-22 Each column represents a separate regression model for each prey species. Intercepts and random effects of site are excluded from the output.



	Wild Boar	Sika Deer	Red Deer
Treatment [Tiger]	-6.11	-1.46	
Time of Day [Night]	1.76	13.17 **	
Obscuring Fabric [Present]	-41.96 ***	-29.01	
Season [2020]	-22.58 **	-7.87	
Season [2021]	-12.76	-5.29	
Number of Adults + Subadults	6.11	3.64 ***	
Number of Juveniles	-41.85 ***	0.63	
Number of Photos	1.48 ***	0.82 ***	0.85 **
Treatment [Tiger]:Season [2020]	18.74		
Treatment [Tiger]:Season [2021]	11.95		
Num.Obs.	96	61	8
* p<0.1, ** p<0.05, ***p<0.001			

Discussion

In analyzing whether olfactory and auditory cues of Amur tiger presence affect ungulate antipredator behavior, I found no highly significant results indicating that such an effect exists. Therefore, I cannot reject the null hypothesis that Amur tigers do not provoke antipredator behaviors in their ungulate prey through olfactory and auditory cues of tiger presence.

However, I did find some weakly suggestive results. At a p-level of 0.1, I found that tiger sensory cues may increase the visit duration for wild boar versus the mesopredator control. By itself, this effect may be counterintuitive, as we might expect that an appropriate antipredator response would be to reduce visit duration, rather than increase it. However, this effect, though weak, may confound the analysis of tiger cues on wild boar vigilance. While the most supported model predicting wild boar vigilance did not include visit duration as a predictor, it did include number of photos, and number of photos was highly ($r=0.78$) correlated with visit duration. As such, the highly significant ($p<0.001$) positive relationship that number of photos had on wild boar vigilance behaviors may partially confound and obscure an effect of tiger sensory cues where wild boar may spend more additive time vigilant in the presence of tiger sensory cues (as opposed to vigilance being compensatory for other behaviors during visits of generally equal duration). The effect of tiger sensory cues on wild boar visit duration is not significant enough to assert this strongly, but it suggests follow-up research to address this potential confounding effect.

I did find additional results of interest outside of the central question. Vigilance was positively correlated to the number of young at a suggestive level ($0.001<p<0.05$), where adult and subadult boar appeared to show 3.73 additional vigilant behaviors per additional piglet. This increased vigilance did seem to come at the cost of foraging, as they also showed 41.96 fewer foraging behaviors ($p<0.001$) per additional juvenile. While vigilance, defined as a multifunctional looking behavior above shoulder height, may indicate an antipredator behavior, that is not necessarily the case. Scanning behaviors may serve social, foraging, or locomotive purposes (74). In this case, mature members of the sounder may be more vigilant in the presence of piglets because of the vulnerability of the piglets to predation, or alternatively because the tendency of piglets to wander and play draws direct parental or social attention from adult and subadult wild boar (103,104,128,129). Without a clear association with any manipulated cue of predation risk, I cannot suggest that one hypothesis is superior to the other. Moreover, the fact that I only have a single visit with piglets during experimental and control conditions makes me cautious about ascribing too much weight to this result.

The presence of the obscuring fabric had a significant ($p<0.001$) negative effect on wild boar foraging, where boar foraged on average 41.96 fewer times in the presence of the obscuring fabric versus without. The presence of the fabric was also significantly ($p<0.001$) positively correlated to increased visit time, where boar spent roughly 13.32 minutes more time at the site when the fabric was present. From the photos themselves, the wild boar spent a great deal of time and effort attempting to tear at and eat this artificial addition to their habitat, behaviors I classified as 'investigative' as opposed to head-down foraging of vegetation. While the obscuring fabric was meant to simulate greater predation risk through obscuring ungulate vision while feeding head-down, the actual interactions I observed instead reflected investigative and consumptive behaviors with the fabric, and so I am not interpreting this correlation in an antipredator context. This interpretation is corroborated by the finding that 'no' carryover effect was positively correlated with visit duration at a suggestive level ($0.001<p<0.05$), indicating that boar may spend 7.58 more minutes at sites without a preceding carryover effect. Since 'no' carryover effect only occurred at the beginning of a season, this suggests that boar may spend more time investigating novel structures in their environment.

Sika deer foraging was positively correlated to nighttime at a suggestive level ($0.001<p<0.05$), where sika deer appeared to demonstrate 13.17 more foraging behaviors per visit at night versus during the day. There was no evidence from the vigilance model that sika deer were less vigilant at night, so it does not appear that this nighttime foraging comes at the expense of vigilance. Therefore, there is no clearly suggestive evidence that sika deer are foraging more at night because they feel safer from predation. However, it may simply be that under cover of darkness, sika deer are less likely to perform other behaviors such as locomotion or investigation and so foraging naturally increases.

The sample size of red deer visits was too small (n=8) to draw any meaningful conclusions from analysis.

Tigers, and Amur tigers in particular, range across large territories. One study found that females in SABZ maintained territories of 390 +/-136 km^2 and males maintained territories of 1385+/-539 km^2 (130). Yudakov and Nikolaev studied snow tracks of tigers in the Russian Far East and found that males travel on average 9.6 km per day and females 7 km per day. These metrics varied markedly, with both the disposition of the individual animal and with prey availability, where tigers in more prey-rich territories would naturally be less likely to make long-distance transgressions in search of prey. Combined with the brief time that Amur tigers are recorded spending at long-term resting sites (defined by hours rather than days or weeks) and the possibility that a large amount of fecal accumulation may indicate a relative satiated tiger less likely to make an immediate predatory attack, and the presence of tiger feces in the forest may well have little significance on whether an ungulate is at risk of attack (103).

Two recent papers indicate that wild boar may display antipredator behaviors in response to risk of Amur tiger attack. Zaitsev (2024) used snow tracking data to investigate how boar spatial organization related to vulnerability to tiger attack in and around SABZ for the period from 1977-2020 (131). He found that boar movement patterns appeared to favor reducing maternal group vulnerability to tiger attack, as compared to lone boars and tuskers, and that boar changed their movement patterns in response to attacks; there was no indication that boar responded to indirect cues of tiger presence beyond visual detection (131). Li et al 2025 tested Amur tiger feces and Amur tiger calls as potential deterrents of wild boar to prevent crop damage in Northeast China (132). The authors tested deployment of fresh tiger feces at the edge of experimental plots and tiger calls played throughout the day. While the authors did find that both measures were effective at repelling wild boar, there are experimental issues preventing strong inference for the effect of in-situ tiger sensory cues on wild boar. First, the authors did not compare the effect of tiger feces to a control fecal sample, rather comparing it to a plot with no countermeasures deployed. Second, while the authors did deploy wolf calls and wild boar distress calls in addition to tiger calls, they did not explicitly compare these treatments to each other or to a hypothesized non-deterrent call, but again to a plot with no countermeasures deployed (132). Thus the effect of biologically plausible tiger sensory cues on ungulate prey remains unresolved, with further experimentation likely needed.

I did not find that adding an auditory playback component to my experimental setup compensated for the loss of sample size in my second and third field seasons, by heightening the strength of the risk cue at my experimental sites. Berger 2007 and Berger et al 2001 found that auditory cues did induce fear responses in Amur tiger prey, but those experiments differed in several critical ways from the work I did here. In those studies, Berger and colleagues used an agonistic call, indicating an animal about to attack (albeit in a defensive manner, rather than a predatory one) while I used long distance advertisement calls, to simulate presence of the vocalizing tiger and conspecific socializing (78,111,116). Despite anecdotes about tigers using roars to imitate or even ‘paralyze’ prey, I remain skeptical of tigers using any vocalization during hunting, and available videos of tiger hunting lend credence to the logical assumption that, as Nobel laureate Wole Soyinka once stated, “A [hunting] tiger does not proclaim his tigritude, he pounces” (133,134). Li et al (2025) did not specify the nature of the Amur vocalizations they used (whether agonistic or social) and also played the calls several times per day, which is biologically implausible given that tigers do not frequently vocalize; this is in addition to the issues with experimental controls mentioned previously (103,105,132). Furthermore, reported effects of predator audio playback on mammalian prey last on the order of minutes, rather than the order of days that my experiment is testing (85,117).

Additionally, I have significant doubts as to whether any ungulates would have heard the calls I played. While I played tiger calls as loudly as possible with a portable speaker, my field tests indicated that humans could not hear them beyond 140 meters or so away. While this does not speak to a larger sample size of humans, much less to ungulate hearing, tiger calls in the region have been heard at scales closer to 1-2 kilometers away by human beings; while the decibel level I used was perhaps even louder than tigers in nature, I was only able to measure decibel level across all frequencies, while papers specifically cite the dB level at 150-200 Hz (116,135). Combined with the likelihood that ungulates in the general area of my sites flee upon my approach before I begin playback, and the dense distribution of streams and rivers (adding more background noise), I find it unlikely that many, if any, ungulates heard the playback.

The absence of clear evidence in favor of behavioral effects of tiger feces on ungulate prey does not preclude other nonlethal effects. Petrunenko et al 2016's research indicated that vegetation cover is significantly associated with tiger kill site location, and Hernandez et al 2005 found that mule deer in a system with pumas abandoned feeding significantly more often in edge habitats (i.e. close to vegetation cover) versus open habitats (55,65). It stands to reason that if tigers move too frequently and too widely for signs of their presence to be a useful risk cue, then a more prudent antipredator strategy could be to increase vigilance and decrease presence in sites that are structurally risky. For example, based off Petrunenko et al 2016, we may hypothesize that ungulates feeding in or immediately next to dense forest are more likely to show frequent vigilant behaviors or abandon feeding than ungulates in open habitats (65).

Miller found that domestic cattle show significant antipredator behaviors in response to a direct sighting of a tiger (81). In the same vein as the above, signs of tiger presence may be so diffuse in the forest and poorly associated with a tiger in the immediate vicinity that it is a poor optimal foraging strategy to be constantly stressed out; therefore it may be more adaptive to avoid obstructive cover and rely on proximal detection of a tiger through a direct visual sighting or other sensory detection.

Recent studies on prey aversion to predator feces indicate that a significant aspect to the aversion is a diet-specific response; prey species may respond particularly strongly when they smell predator feces containing a conspecific (136,137). Cox et al 2010 found that eastern grey kangaroos showed significant aversion to tiger scat after tigers had fed on kangaroo meat, despite kangaroos being evolutionarily naïve to tigers as predators (138). The zoo tigers from which I obtained feces primarily ate domestic meat such as chicken and beef, with rare inclusions of deer. Studies out of Poland that partially inspired this project did not report the proportion of predator (lynx and gray wolf) diets that included the wild prey being studied, but Wikenros et al did indicate that wild ungulate carcasses as a regular component of their lynx's diets (77,101). As a result, the scat I used may have lacked the perceived threatening volatiles that trigger antipredator behaviors in ungulates. Other olfactory cues, such as urine sprays, may also contain different and potentially more informative volatiles for prey species.

If tigers structure ecosystems through top-down behavioral effects, then better study may go towards analyzing antipredator behaviors in structurally risky microhabitats or with simulated visual presence of a tiger. Alternately, because tigers are known to depress wolves in the Russian Far East, evidence from this study and the body of literature on wolf nonlethal effects on prey indicate that tiger presence may change the landscape of fear largely though their local extirpation of wolves, rather than by replacing wolf cues with tiger cues; that is, potentially inducing trophic effects by the suppression of a subordinate predator (53,63,139–141).

Chapter 3

Modelling potential Effects of ASF on Amur tiger Carrying Capacities and Quasi-extinction risks in Northeast Asia

Introduction

Disease-induced losses to wildlife can have significant effects that resonate throughout the larger ecosystem. For example, after rinderpest decimated native ungulate populations, wildfires raged in East Africa in the late 1800s due to the accumulation of uneaten plant biomass (49). White-nose syndrome-induced reductions in Wisconsin bat species were associated with a relative increase in their preferred arthropod prey species (142). Population decline in the Tasmanian devil (*Sarcophilus harrisii*) due to devil facial tumor disease induced a decline in eastern quolls (*Dasyurus viverrinus*) by way of mesopredator release of feral cats (*Felis catus*) (143). These examples highlight the urgency of reacting to novel or spreading diseases to not only anticipate the potential consequences, but also to potentially intervene when an infected species has a strong interaction with a species of conservation concern. Therefore, the ongoing African swine fever (ASF) epidemic in Eurasia poses a potentially significant threat to Amur tiger (*Panthera tigris*) populations in northeast Asia by greatly reducing densities of a preferred prey species, wild boar (*Sus scrofa*) (104,114,144–147). In this study, I aim to assess the relative risk that ASF may pose to Amur tigers population viability across their extant range.

ASF is a highly lethal infectious disease, affecting several wild and domestic suid species, including the wide-ranging wild boar (148–150). Affected animals are characterized by lethargy, respiratory distress, and anorexia among other symptoms, and acute strains possess lethality approaching 100% (114,151). Highly stable at low temperatures, the virus (ASFV) is transmitted by direct and indirect contact with conspecifics (including carcasses), in aerosol form at short distances indoors, as well as potentially via arthropod vectors such as soft ticks or stable flies (151–153). Regionally, the disease spreads both through management and transportation of domestic pigs, as well as through wild-living pig herds, especially wild boar in Eurasia (151,154). As of fall 2024, there is no safe and effective vaccine available, though several are in development (155).

While endemic to sub-Saharan Africa, outbreaks of ASF in Eurasia were documented as early as 2007 (148,155). By 2019, researchers had detected a highly lethal (genotype 2, 94.5-100% mortality rate) strain of the African Swine Fever Virus (ASFV) in the Russian Far East (114). That was followed by reported outbreaks in both wild boar and domestic pigs throughout the region by December 2020 (114,156). Zakharova et al estimated that, resultant from expected wild boar population decreases, total ungulate biomass in the Russian Far East (Comprised of the following federal districts: Amur Oblast, Jewish Autonomous Oblast, Khabarovsk Krai, Primorsky Krai) may drop by 8.4% (95%CI: 4.1-13.0%) and in Primorsky Krai alone by 33.6% (95% CI: 19.3-46.1%) (114).

ASF and Tigers

The effect of ASF on tiger prey is of special interest because the ongoing ASF epidemic spans most, if not all, of the extant range of the endangered Amur tiger, across both the Russian Far East and northern China (87,149,157–160). Wild boar comprise perhaps the single most important component of Amur tiger prey, accounting for as much as 55% of tiger diet by biomass in Hunchun Nature Reserve in Northern China, and contributing consistently over 30% of their diet by biomass in other areas of Amur tiger range where they co-occur at stable densities (104,129,147). In these studies, tigers show a significant preference for wild boar relative to their abundance on the landscape (104,129,147). This seems consistent with southern areas of tiger range, as calculated by Hayward et al (146). Miquelle et al 2010 suggest that because wild boar forage loudly with their snouts inclined closely towards the ground, they are disproportionately vulnerable to unseen approach from a stalking tiger (161). Together with red deer (*Cervus canadensis*), wild boar are the most strongly preferred prey species for Amur tigers, being considerably larger than other common ungulates in northeast Asia (161). While tigers are generalist predators, it is likely energetically favorable for them to prey on large-bodied animals close to their own weight, rather than considerably smaller species such as sika deer (*Cervus nippon*) (102,146,161).

Data from Sikhote-Alin Biosphere Zapovednik, situated roughly in the center of extant Amur tiger range (Figure 1), suggests that between 2020 and 2021, wild boar biomass decreased by almost 99%, while recovering up to ~12% of pre-ASF levels in the next year (123,162). Although local veterinary technicians did not conduct large-scale necropsies to investigate the cause of wild boar deaths, local reports of boar carcasses indicating poor (diseased) condition at time of death, as well as Zakharova et al's spatiotemporal analysis of ASF outbreaks strongly suggest that the major factor in suid mortality was ASF (114).

Large Carnivore Functional Responses to Prey Depletion

It is well established that large carnivore densities are positively correlated with prey densities, such that the biomass of prey energetically limits the biomass of predator populations it can support (163,164). The exact mechanism by which prey depletion affects large carnivores is less clear. If we take the example of tigers, there are several hypothetical mechanisms by which they may be demographically limited by prey depletion. Tigers with insufficient prey may starve; following Miller et al's work showing that tigresses with cubs have the highest caloric needs, this may increase either breeding female mortality or cub mortality (102). Tigers may start attacking riskier prey, whereby their mortality risk from hunting increases; this may include more formidable prey such as brown bears (*Ursus arctos*), or domestic prey that brings tigers into closer contact with humans that pose the greatest mortality threat to tigers (147,165,166). Tigers may expand their territory size (territory defined in this study as individual home range), reducing density across available habitat; Correlational studies across sites support this relationship, but within-site it is less clear how flexible tigers are to expanding and contracting their territories (130,164,167). Tigers could more frequently engage in intraspecific territorial conflict or longer-range dispersals in order to obtain territories with sufficient available prey; these behaviors are correlated with higher mortality (130). This list of potential mechanisms highlights the breadth of analytical approaches that conservationists and scientists may take in predicting how prey depletion may affect tiger populations.

Prior studies of tiger responses to prey depletion have consequently varied in their approach. Barber-Meyer et al 2013's study of tiger occupancy found a negative correlation between tiger occupancy and prey-depleted cells in the Terai Arc Landscape (TAL) of Nepal, but the mechanism is again unclear (168). Karanth and Stith 1999 proposed that cub mortality would rise in response to prey depletion, but lacking data to inform such an effect, they modeled tiger population dynamics with a range of potential cub mortalities, projecting hypothesized effects on the demographic structure of a tiger population (169). Carter et al 2019 used the energetics models derived by Miller et al 2014 to construct an agent-based model, assuming that insufficient prey would lead to female starvation (and therefore cub death) (102,170).

Studies on lions (*Panthera leo*) and wild dogs (*Lycaon pictus*) suggest that prey availability may directly affect fecundity (171–173). Marneweck et al 2019 found that wild dogs bred at younger ages when prey availability was high(171). Schaller found that sex contacts between lions and lionesses were positively correlated with prey density, and Vinks et al 2021 found that both cub recruitment and pride size among lions were negatively correlated with prey density (171,172). However, given that lions and wild dogs are gregarious and tigers are largely solitary, extrapolating these observations to a tiger model seems incautious (105,172).

Approach

As of 2024, ASF has been detected in wild suids throughout much of the Asia-Pacific region, indicating that tigers may be affected by ASF-induced prey depletion throughout much of their range (149,150,174,175). Tigers remain endangered and a landscape-wide threat to their food base is of critical concern for tiger conservation (160,168–170,176,177).

Here I set out to (i) simulate changes to adult tiger carrying capacities in four disparate Amur tiger habitats under ASF also (ii) to simulate tiger population trajectories in these habitats with a stochastic stage-structured population model to compare population viability with and without ASF. For each habitat, I simulated three different post-ASF outbreak scenarios in addition to a 'No ASF' baseline to account for uncertainty in the long term effects of ASF on wild boar populations: boar populations remaining depressed, wild boar populations steadily recovering, and wild boar populations artificially depressed by management culling aimed at slowing the spread of ASF (114).

Wild boar make up a greater proportion of available prey biomass in northern areas of Amur tiger distribution than in more central and southern area(104,123,128,147,178).I therefore hypothesize that (i) in more northern areas of Amur tiger habitats (i) we will see more severe reductions in tiger carrying capacity in ASF simulations and (ii) following this prey depletion, Amur tiger population simulations in more northern areas will show a commensurately higher increase in relative quasi-extinction. This is the first step in assessing whether and to what extent different tiger populations are likely to experience significant demographic setbacks due to wild boar depletion (179).

Methods

1. Protected Areas and Prey Biomasses

I used published ungulate prey biomass data from four sites in Amur tiger range (pre-ASF) to set baseline estimates of prey density pre-ASF. These estimates included densities of wild boar, red deer, sika deer, and roe deer (*Capreolus pygargus*). I used ungulate density estimates from Khinganskiy Zapovednik (KZ) collected between 2013 and 2014, from the Eastern Wanda Mountains (EWM) collected in 2002, from southern Russia collected during 2008-12, and from Sikhote Alin-Biosphere Zapovednik (SABZ) collected during 2020-22 (104,123,128,178). While many of these prey density estimates are years-old, they represent the best data available on typical ungulate densities in the region prior to ASF. Figure 1 shows the locations of these sites.

In their survey of prey abundances in southern Russia, Kerley et al 2015 indicated that their study area overlapped with land that was later incorporated into Land of the Leopard National Park. Therefore I applied their estimates of ungulate density to the area covered by Land of the Leopard National Park and the contiguous smaller park Kedrovaya pad (LotL+KP) (104). Kerley et al only reported relative abundances of the primary ungulate prey species. To calculate reasonable ungulate biomass, I assumed that roe deer occurred at similar individual densities in Land of the Leopard as they do in SABZ and using that as an index, I derived estimates for wild boar and sika deer densities (104). I detail this procedure further in Appendix 3, section A.

The site highlighted in Figure 1 as the Eastern Wanda Mountains is in fact Raohedongbeiheisfeng National Nature Reserve; however, I did not use the park's full area of coverage to inform biomass estimates as it was unclear to what extent Zhang et al's 2002 survey of prey biomass overlapped with park coverage and how much of the total park is suitable tiger habitat. I therefore treated only the 5393 km^2 area that they covered in their survey as potential tiger habitat, and I labeled the

Raohedongbeiheisfeng National Nature Reserve as a coarse indication of the location of the Eastern Wanda Mountains (178).

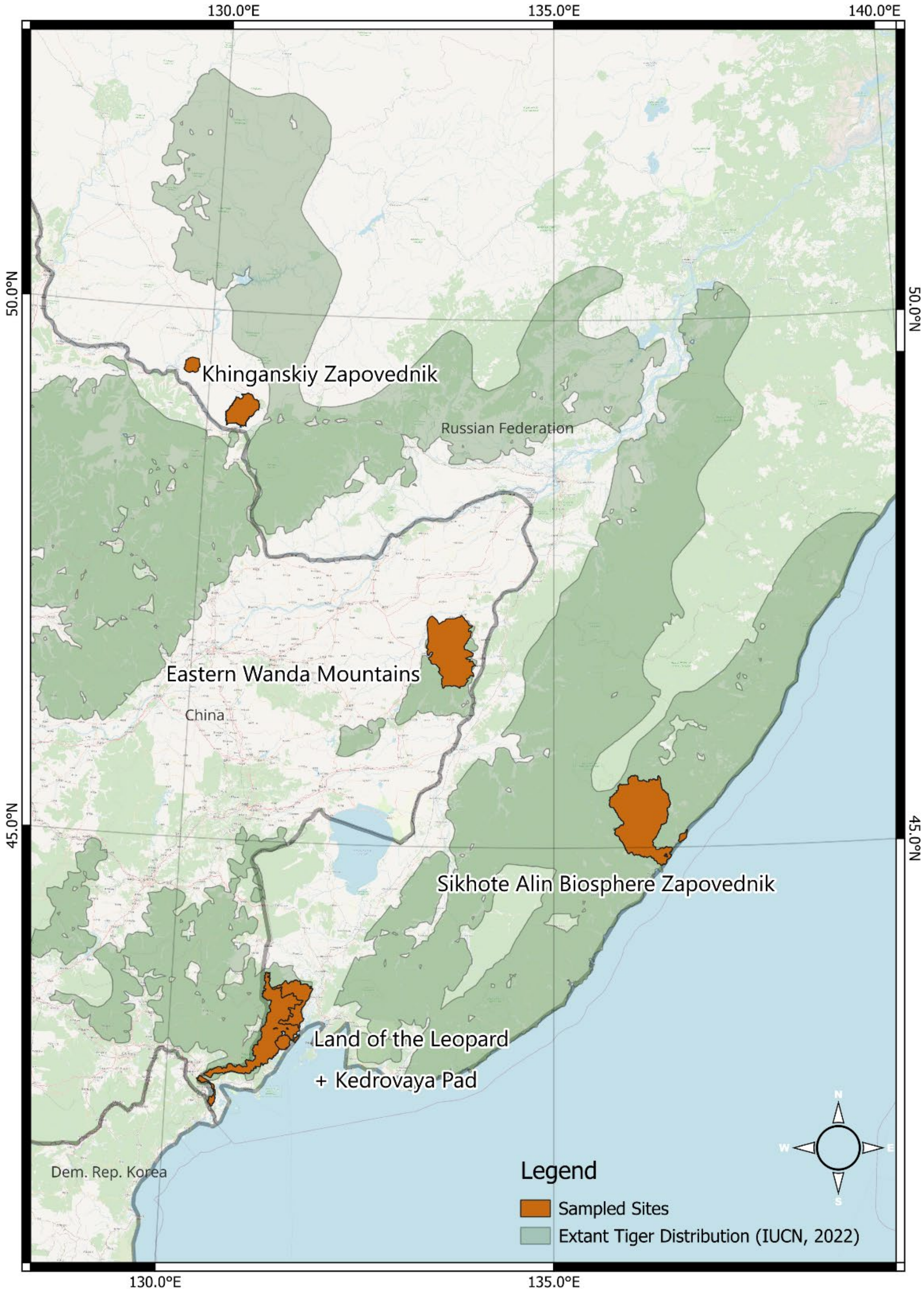


Figure 1: Location of the four representative sites used to analyze potential demographic impacts of African Swine Fever (ASF) on Amur tigers (*Panthera tigris*) in northeast Asia.

2. African Swine Fever Scenarios

The prevailing literature on African Swine Fever does not detail population dynamics of wild boar post-ASF outbreak; indeed, much of the literature discusses culling boar to keep their populations low in order to reduce the spread of ASF into domestic pigs and pork supply chains (114,180–182). To address this uncertainty, I simulated three different ASF scenarios (ASF+Recovery, ASF+Depressed, ASF+Cull) to compare with a baseline scenario where there is no ASF. In each ASF scenario I reduced each habitat's wild boar to 5% and 13% of their pre-ASF biomass in years one and two respectively, based off data collected from SABZ (123). For the ASF+Recovery scenario, I simulated an annual wild boar population growth rate of 9% after the second year of ASF, approximating boar demographic parameters reported from moderate winters and intermediate masting frequency (183). For the ASF+Depressed scenario, I simulated wild boar biomasses remaining depressed at 13% of pre-ASF levels after the first two years of ASF, in the case that the virus remains endemic, virulent, and lethal (184). For the ASF+Cull scenario, I simulated human-induced suppression of wild boar populations at a density of .025 individuals/km^2 after the first two years of ASF. That level of suppression follows Russian federal guidelines for halting the spread of ASF, though it is not clear if the Russian government has implemented this intervention (114).

3. Tiger Carrying Capacity

I estimated adult tiger carrying capacity using Miquelle et al's regression relating Amur tiger population density in SABZ to prey biomass (Equation 1) (161).

$$Equation\ 1: \quad T = 0.0009 * P + 0.0623$$

Where T is adult tigers/100km^2 and P is prey biomass (kg/km^2). I found that this equation, parameterized entirely on the Amur tiger population in SABZ gave more reasonable estimates of adult tiger carrying capacity than alternate equations trained on data from south and southeast Asia, where prey biomass is much higher than in Russia (161,178). I also note that there is an error in Miquelle et al's transcription of this equation, confirmed with the lead author (D. Miquelle, personal communication, January 4, 2025), where the y-intercept is written as .623, but by inspection of Figure 13.4, it is clear that this should be .0623 (161).

4. Stochastic Stage-Structured Tiger PVA with Density Dependence

I constructed a stage-structured matrix model (Figure 2) of Amur tiger population dynamics to simulate the effects of prey depletion through a reduction in carrying capacity. I followed the example of Morris and Doak 2002 in incorporating density dependence solely as a reflective ceiling where transients (subadults) can only transition to becoming breeders (adults) when there are unoccupied territories; the total number of territories available depends on the prey-derived carrying capacity from equation 1 (185). When carrying capacity drops in the model, the probability of a transient becoming a breeder reduces; if the number of breeders exceeds the carrying capacity, then 'surplus' breeders become transients again until vacant territories emerge. As with other stage structured tiger population viability analyses (PVAs), I considered females to be the limiting sex and restricted my model to modelling female tigers only across all age-classes (157,186).

The vital rates I used are in Table 1 alongside the sources from which I derived them. I modeled environmental stochasticity using a coefficient of variation of 0.05 for survival and fecundity, after Tian et al (157). I used beta distributions for survival and a normal distribution for fecundity; I imposed a minimum fecundity of 0 female cubs per breeder per year and a maximum of 4 female cubs per breeder per year for biological plausibility (187). I derived female breeder carrying capacity from total adult carrying capacity by assuming a ratio of 5:3 adult females to adult males and then rounding to the nearest whole tiger (157).

I initiated all tiger simulations with the maximum possible number of pre-ASF female breeders, zero transients, zero juveniles, and with 1.13 cubs per female. I derived the adult female to cub ratio from historical population records of Amur tiger censuses in SABZ (162). I rounded all tiger numbers up or down to the nearest whole tiger (i.e. a decimal tiger of .5 or above rounds to 1 tiger, and below rounds to 0 tigers). This is a more generous rounding scheme than truncating decimals down to the nearest whole tiger, contributing to this being a 'best-case scenario' modeling exercise for effects of prey depletion on tiger numbers.

I ran all population models in MATLAB 2024b for 10000 iterations. I simulated 10 years, or 2 tiger generations, to avoid far flung extrapolations while still allowing for extended persistence of African Swine Fever in the region (188). I used a quasi-extinction threshold of 2 tigers to end simulations prematurely, considering only two females of any sex-age class to be a catastrophic scenario (189) . I chose to report results as the difference in quasi-extinction probabilities between each ASF scenario and the baseline no-ASF scenario to emphasize the relative quasi-extinction risk of competing scenarios, rather than to offer an absolute prediction (190–192). That is, if the probability of quasi-extinction after 10 years for the baseline no-ASF scenario was 10%, and the probability for the ASF+Cull scenario was 15%, the relative quasi-extinction probability for the ASF+Cull scenario would be +5%.

This is likely a conservative modeling effort, as I am restricting my modeling to sites in and around protected areas, where ungulate densities and tiger vital rates are likely higher than in the surrounding landscape (186).

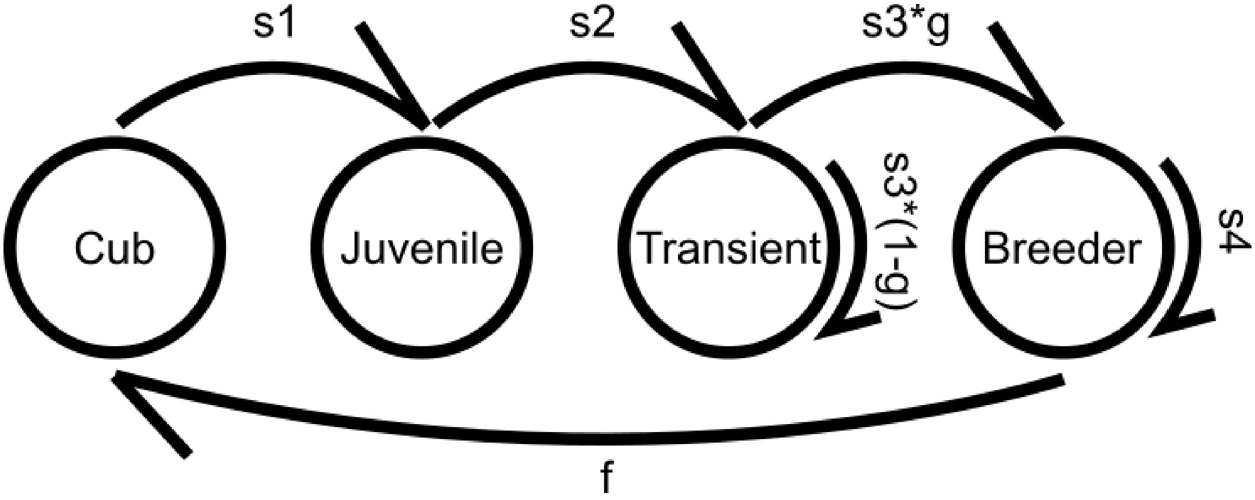


Figure 2: Stage Structured Model of Amur tiger population dynamics (females only). Stages: cubs (0-1 years old), juvenile (1-2 years old), transient/subadult (2+ years old without a territory), breeder/adult (3+ years old with a territory, capable of breeding). s1 and s2 are the survival probabilities from cub to juvenile and juvenile to transient respectively. s3 and s4 are the survival probabilities for transients and breeders. g is the probability that a transient tiger can become a breeder based on the number of unoccupied territories and the number of transients.

Table 1: Vital rates for Amur tigers. All parameters for females only.

	Estimate	Source
Cub (0-1 yrs) Annual Survival	0.56	(187)
Juvenile (1-2 yrs) Annual Survival	0.8	(157,193)
Transient (2+ YRs, No territory) Annual Survival	0.552	(166)
Breeder (3+ yrs, With territory) Annual Survival	0.847	(166)
Breeder fecundity (Female Cubs per breeder per year)	0.7	(187)

Results

1. Prey Biomasses and Carrying Capacities

Tiger carrying capacity in Sikhote Alin Biosphere Zapovednik dropped from 17 adults to ~15-16 adults across ASF simulations, which meant going from 11 female territories (pre-ASF) to 9 female territories in the worst years of ASF. In Khinganskiy Zapovednik, the already low carrying capacity dropped from 4 adults to ~2 adults across different ASF scenarios, meaning that female adult carrying capacity dropped to just a single animal. In the Eastern Wanda Mountains, tiger carrying capacity dropped from 8 adults to 6 adults, whereas in Land of the Leopard and Kedrovaya pad, the tiger carrying capacity dropped modestly from 6 adults to 5-6 adults across ASF scenarios. More detailed plots of tiger carrying capacity over time by scenario are in the Appendix 3 (Figures A1-A4).

2. Effects of wild boar biomass reduction on Amur tiger population viability

None of the ASF scenarios in SABZ resulted in a notable increase in quasi-extinction probability over baseline (Figure 3).

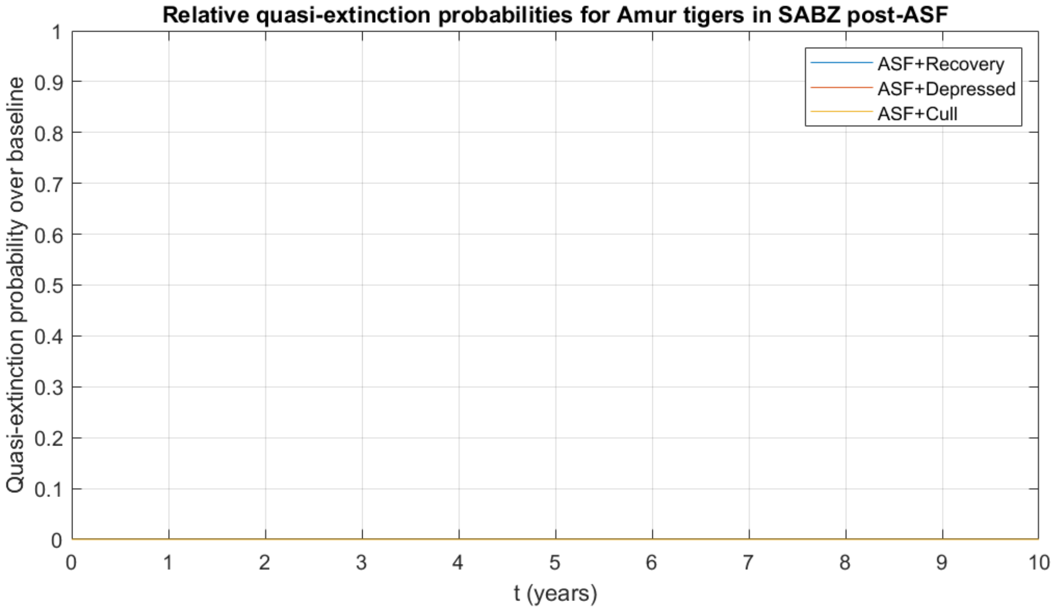


Figure 3: Relative quasi-extinction probability for Amur tigers in Sikhote Alin Biosphere Zapovednik (SABZ) under different African Swine Fever (ASF) scenarios. All scenarios are plotted as the additional quasi-extinction probability above the baseline scenario of no ASF. All relative quasi-extinction probabilities are close to 0 in SABZ.

On the other end of the spectrum, quasi-extinction probability relative to baseline increased dramatically across all ASF scenarios in KZ (Figure 4). Quasi-extinction probability was more than 25% higher in ASF scenarios than the baseline scenario after 4 years and approximately 65% higher after 10 years.

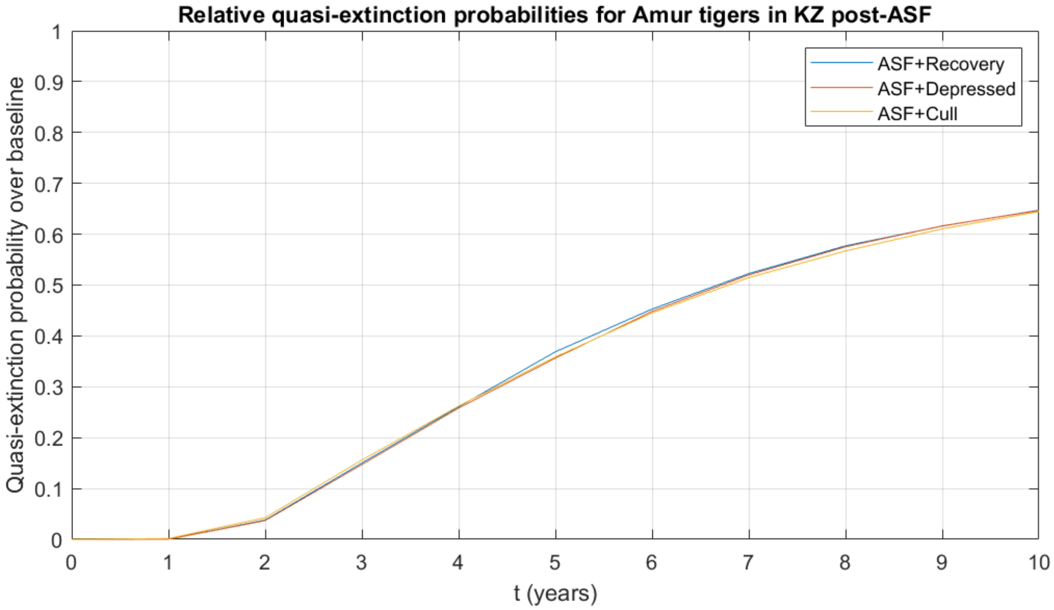


Figure 4: Relative quasi-extinction probability for Amur tigers in Khinganskiy Zapovednik (KZ) under different African Swine Fever (ASF) scenarios. All scenarios are plotted as the additional quasi-extinction probability above the baseline scenario of no ASF.

Simulated tiger populations in both EWM (Figure 5) and LotL+KP (Figure 6) showed more moderate increases in quasi-extinction probability over the baseline scenario. EWM tiger populations showed ~2% increase in relative extinction risk over baseline after 10 years, and LotL+KP tiger populations showed increased extinction risk over baseline of ~7% after 10 years. Figures A5 and A6 in Appendix 3 show more zoomed in plots for tiger populations in EWM and LotL+KP.

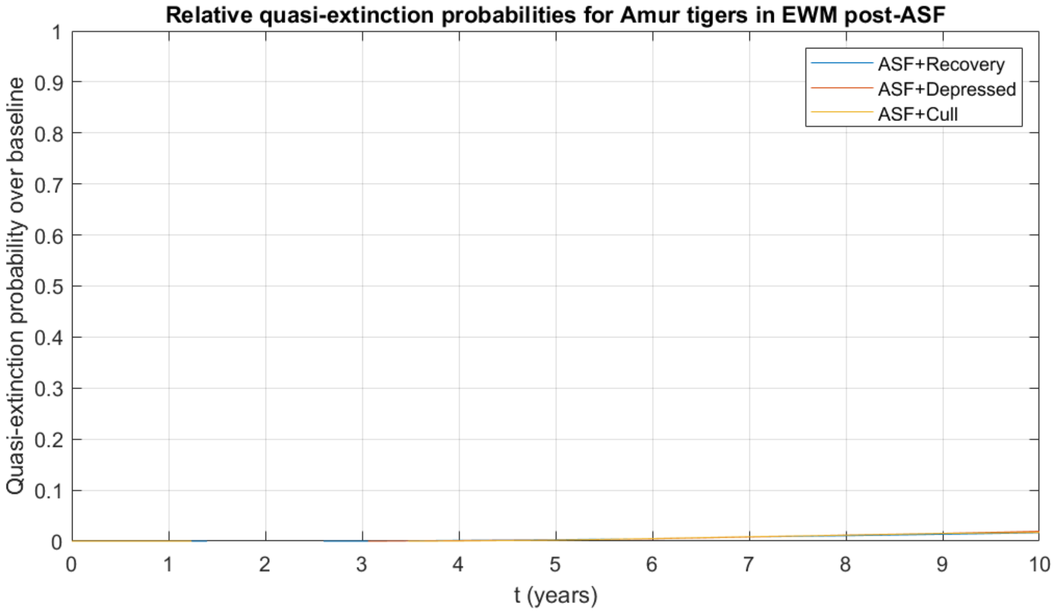


Figure 5: Relative quasi-extinction probability for Amur tigers in the Eastern Wanda Mountains (EWM) under different African Swine Fever (ASF) scenarios. All scenarios are plotted as the additional quasi-extinction probability above the baseline scenario of no ASF. See Figure A5 in Appendix 3 for a truncated plot showing each scenario more clearly.

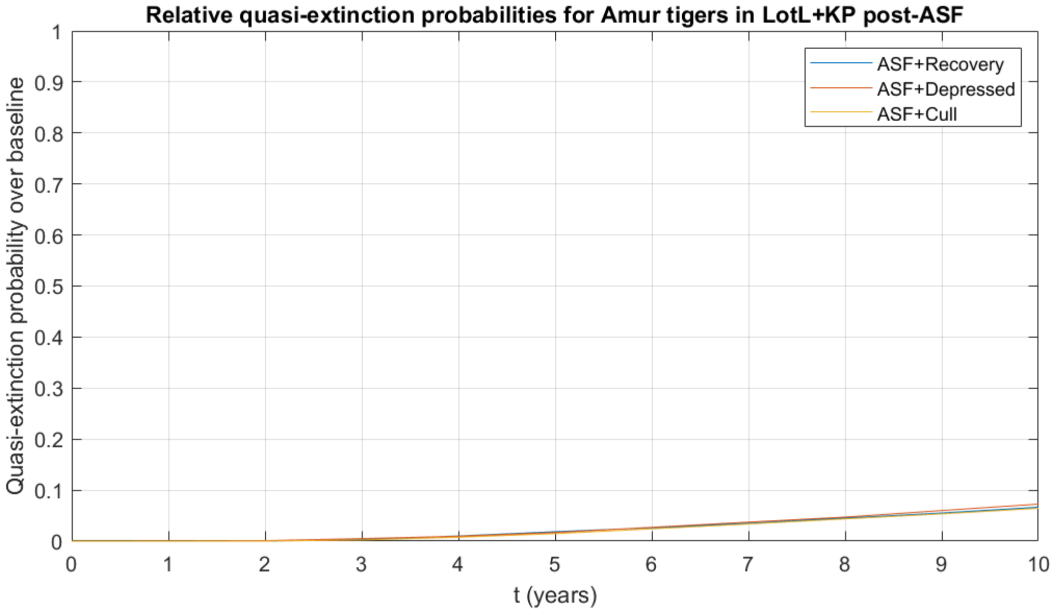


Figure 6: Relative quasi-extinction probability for Amur tigers in Land of the Leopard and Kedrovaya Pad (LotL+KP) under different African Swine Fever (ASF) scenarios. All scenarios are plotted as the additional quasi-extinction probability above the baseline scenario of no ASF. See Figure A6 in Appendix 3 for a zoomed-in plot showing each scenario more clearly.

Discussion

I find evidence supporting the hypothesis that Amur tigers at the northern edges of their range are significantly more vulnerable to significant decreases in carrying capacity in response to ASF-induced prey depletion compared with sub-populations in southern and central areas of Amur tiger range. I also find evidence that these northern populations of Amur tigers face a commensurately increase in quasi-extinction risk in response to wild boar prey depletion. Tiger populations in KZ, at the very northwest of Amur tiger range, show particularly strong vulnerability to perturbations to their prey base, with up to a 70% higher relative risk of extinction under ASF scenarios versus baseline simulations with no ASF. This comes as little surprise, as wild boar constituted over 72% of the available prey biomass reported in KZ, and the effects of prey depletion are compounded by the relatively small footprint of this reserve (970 km^2)(128). Simulations of ASF-induced prey depletion in the EWM as well as LotL+KP showed noticeable but modest increases in quasi-extinction risk relative to baseline. The relative abundance of red deer in EWM and sika deer in LotL+KP as well as the larger areas of these protected areas helped buffer the effects of wild boar depletion across simulations(104,178). In Sikhote-Alin Biosphere Zapovednik, the only site with all four primary ungulate prey present (wild boar, red deer, roe deer and sika deer), ASF showed no notable additive effect on quasi-extinction rate.

In the case of SABZ, it should also be noted that ungulate density estimates showed an apparent increase in red deer density concurrent with wild boar density decline (123). It is not clear if the inverse population trends between red deer and wild boar observed in SABZ from 2020-22 were related to some form of competitive release, or if it was merely coincidental, but it suggests a compelling direction for study especially as relates to Amur tiger population viability and the opportunity to prey switch without an energetic cost (123).

Between scenarios, the ASF+Cull scenario (where managers follow Russian federal guidelines and maintain wild boar at or below densities of 0.025 individuals/km^2) showed the largest increase in relative extinction risk for simulated tiger populations, but the marginal effect over the ASF+Recovery (boar recover at a rate of 9% per year) and ASF+Depressed (boar do not recover beyond 13% of pre-ASF populations) was not marked over the 10 year duration of the simulation.

Although tigers are generalist predators that prey upon a wide range of ungulate prey, like other solitary felids they prefer large-bodied prey species with individuals similar in bodyweight to tigers themselves (146). In sites without robust red deer populations, ASF may force greater energetic expenditure and a higher likelihood of starvation from all adult and subadult tigers if they are forced to hunt smaller bodied sika and roe deer at higher rates (102,161). As mentioned in the methods, this was a conservative modeling effort, due to the focus on protected areas where ungulate densities and tiger vital rates are likely higher than elsewhere on the landscape (186). Recommended follow ups to this work include metapopulation modeling to incorporate the entire landscape, as well as consideration of potential functional effects on tigresses with cubs, and combining the effects of prey depletion with increased conflict mortality.

One unmodeled consequence of the sudden drop in available prey is that a tiger that is unable to effectively meet caloric needs with wild prey or unable to acquire a territory may shift to domestic prey; Khorozyan et al 2015 analyzed a meta-data set across big cat species and found that big cat predation on domestic prey was strongly negatively predicted by wild prey biomass (194). Tkachenko, reporting out of Bol'shekhekhtsirskii Reserve in Khabarovsk Krai (again at the northern edge of Amur tiger distribution) reported a drastic shift in a tigresses diet that was reportedly unable to kill wild prey due to injury, and shifted largely to dogs (85.7%) between 2000 and 2005; while the barrier to wild prey was hunting ability rather than landscape availability, it demonstrates behavioral plasticity of tigers under food stress to resort to behaviors likely to increase human-wildlife conflict (147). Cheng et al showed that Amur tiger contact with humans and predation on domestic animals were both positively correlated with local prey scarcity (195). As these prior studies suggest, it appears that human-tiger encounters and domestic animal predation by tigers may indeed be sharply increasing post-ASF, as reported in both popular press and peer-review sources (196–198).

A significant concern following the observed uptick in human-tiger encounters in Russia is the possibility that anthropogenic killing of tigers will increase in response. Retaliatory killing of large carnivores, including tigers throughout their range, is a significant threat to their persistence (5,199,200). Tigers that visit villages and kill domestic animals could compound the demographic effects of prey depletion if humans respond by killing tigers, increasing extirpation probabilities by magnitudes beyond what I have projected here. Lukarevskiy et al 2024 reported a strong association between human-tiger conflict and combined tiger death and removal from the wild in Khabarovsk Krai from 2016 to 2023, with a sharp spike during 2022-23 (198). Research has demonstrated that tigers, contrary to prior beliefs, are sensitive to additive anthropogenic mortality, and tiger populations squeezed by both prey scarcity and human persecution may stand little chance of persistence (169,176). Moreover, anthropogenic injuries to tigers are strongly associated with tigers that attack humans, potentially creating a vicious cycle of conflict (165,201). Therefore, my simulations do not adequately account for prey-switching to domestic prey, which likely underestimates quasi-extinction risk due to increased anthropogenic mortality.

I recommend: (i) That managers and scientists urgently complete assessments of ungulate densities in protected areas throughout northeast Asia to update our understanding of where tigers are expected to be under the greatest pressures of prey scarcity (ii) Where prey is critically low I recommend exploring reducing the scope and magnitude of permitted large ungulate hunting, though I understand that this is inextricable from the complications of local sociopolitical and economic conditions. Nevertheless, a temporary moratorium on deer hunting in targeted areas may be the difference between Amur tiger persistence and range contraction. I am cautious about the introduction of wild prey to supplement prey-scarce areas as the effects may be unpredictable; range expansion of sika deer, for example, has been associated with severe reductions in red deer biomass, likely due to competitive exclusion (202). However, more careful or targeted introductions (for example, adding sika deer to parts of their historical range lacking other medium-large cervids) may prove fruitful. Using available prey and conflict data in the Russian Far East, it may be possible to use Khorozyan et al 2015’s methods to identify threshold goals for wild prey biomass density to reduce the likelihood of tiger predation on domestic prey (194). (iii) Targeted investment by state and NGO actors in both research and implementation of human-tiger conflict mitigation and prevention strategies. Goodrich et al 2010 advocated for a variety of zoning and livestock management strategies, the increase of wild prey and anti-poaching measures (203). Cheng et al 2024 advocated for the development of risk maps to inform spatiotemporal management of human-tiger conflict (195). With the currently elevated rate of human-tiger conflict in Russia, there may be sufficient sample size to analyze where and when these conflicts take place to develop a more targeted map of risk that informs site-specific conflict prevention (195).

Culling wild boar in areas infected with ASF aims to reduce transmission of the disease to domestic pigs to safeguard the supply chain of porcine products (182) (180). It is intended to enhance food security, but as shown here, depressing boar populations does not seem to be an effective conservation strategy for wild boar or their predators. Research out of Estonia suggests that aggressive wild boar hunting quotas post-ASF was associated with gray wolves (*Canis lupus*) beginning to ingest energetically trivial plant matter in significant proportions, possibly as a result of prey scarcity (181). I advocate relying on nonlethal measures for both food safety and wildlife conservation; examples include wild boar carcass removal and farm-side prevention of contact between wild and domestic pigs until an ASF vaccine has been approved (155,204–206).

The fortress model of tiger conservation has in many ways been a tremendous success across tiger range (207). However, it is clear that protected areas in isolation are unlikely to support Amur tigers across their range and it is therefore incumbent upon decision makers to expand and intensify work outside of protected areas to study and support the persistence of the Amur tiger. As seen in this study, none of the sites analyzed could sustain greater than 25 breeding females entirely within the protected area, a standard put forth by Walston et al for defining a tiger source site (189). As such research and conservation of Amur tigers in the human-shared matrix between protected areas is a crucial priority if we hope to maintain the health of their populations in coexistence with our own.

Conclusion

While large carnivore populations differ markedly in their ecology and their political context, many research and management interests are conserved across taxa. In this dissertation, I explored three case studies on carnivore monitoring, ecological function, and threats to persistence with the goal of presenting a broad view of large carnivore biology and management and in so doing, building a diverse and relevant skillset for preserving and managing large carnivore populations.

In Chapter 1 I analyzed how the Wisconsin Department of Natural Resources (DNR) has used participatory science to help census wolves in the state via winter wolf track surveys. Analyzing the winter wolf counts done by volunteers and DNR between 2003 and 2011, I found strong evidence supporting the inference that volunteers counted 83% as many wolves as DNR professionals on average. Simulating both volunteer and DNR trackers counting all blocks in all years produced larger plausible ranges of wolf count than uncertainty reported in past DNR wolf reports. Because the usage of volunteers and their relative contributions have changed over time, I concluded that any analysis of Wisconsin wolf population dynamics must be either be partitioned into methodologically consistent time series, or the effect of observers and changing methodology on wolf count must be explicitly accounted for in statistical analysis. I also recommended that the DNR investigate the cause of this discrepancy and increase the transparency of current wolf population reports to support independent analyses such as this one.

In Chapter 2, I investigated whether Amur tigers provoke nonlethal effects in ungulate prey through cues of their presence, namely olfactory and auditory. While I have doubts that ungulates on the landscape heard my auditory cues, I did find weak evidence that wild boar may react to cues of tiger presence by increasing visit duration, which may confound detection of a vigilance effect of tigers on wild boar. I also found evidence that wild boar may be more vigilant with juveniles present, which may indicate that intrinsic group vulnerability is as or more important to antipredator behavior than cues of predator presence. I hypothesized reasons that tiger feces may be uncorrelated with risk of tiger attack, including the wide-ranging and itinerant nature of Amur tigers and the likelihood that microsite characteristics may be far more informative of predatory risk than fecal accumulation. I suggested experiments to pursue these alternate hypotheses of fear of tigers, especially camera trap experiments in sites with varying levels of vegetative cover where high cover would simulate sites where tigers could better approach ungulates unseen. I also discussed potential implications of contrasting landscapes of fear between tigers and wolves, given that tigers suppress and even eradicate wolves where they co-occur (100,139,208).

In Chapter 3, I modeled how Amur tiger populations may respond to widespread prey depletion as a result of African Swine Fever (ASF) induced wild boar mortality. Using a stochastic stage structured model, I simulated quasi-extinction risk for four different Amur tiger populations using three hypothetical scenarios for ASF versus a baseline of no ASF. I found evidence supporting the hypothesis that tiger populations in the northern portions of their range, where wild boar make up a greater proportion of available prey biomass, face the largest increased risk of quasi-extinction. I noted that even in areas of tiger range where there are robust populations of sika deer, the smaller individual biomass of sika deer may impose an energetic cost on tigers to hunt more frequently (102). Moreover, I noted that using vital parameters from tigers in protected areas made the exercise conservative with respect to tiger demographic viability, even ignoring the reported increase in human-tiger conflict associated with ASF in Russia, which may lead to increased poaching mortality (209,210). I recommended a concerted effort by managers to monitor local ungulate populations with an eye towards intervening in catastrophes such as this, as well as a broader landscape level conservation strategy as a complement to fortress conservation, especially in landscapes with small, isolated protected areas such as the NW range of Amur tiger territory. I also made suggestions about future, more complex modelling approaches to this problem, especially in the context of alternate hypotheses on the mechanism of how prey depletion may affect large carnivores. Suggestions included following modeling exercises such as those undertaken by Karanth and Stith 1999 or Carter et al 2019 to investigate effects on lower fecundity or breeding female starvation (169,170).

Human-carnivore coexistence proves challenging in the face of expanding human footprints and multifaceted threats to carnivore persistence (5,177,211). However, we have an increasingly diverse and sophisticated toolkit to both analyze carnivore populations and their influences, to monitor carnivore populations, and to mitigate threats. Provided local and political will, as well as transparent and cooperative efforts, I believe it is both feasible and valuable to do so, and I hope that the research presented here can be a small part of that effort.

Appendix 1

A: Survey Block Alterations

Below I detail all the ways in which I altered the shape of Winter Wolf Track Survey Blocks as given to me by Shannon McNamara via GIS shapefiles. I went through them in reverse chronological order, and they are listed here in the same order. Therefore a change made in 2010-11 is relative to the raw file, while a change made in 2009-10 is relative to the blocks as finalized for 2010-11. I ultimately found 3 periods of survey block stability for the purposes of my analysis: Winter 2010-11, Winter 2006-07 to Winter 2009-10, and Winter 2003-04 to Winter 2005-06. Therefore the major changes in survey blocks occurred in 2005-06, 2009-10, and 2010-11.

Rules: (1) I judged whether the difference in apparent survey block size/shape was significant or possibly due to resolution differences between figures/shape files; I was conservative and did not edit survey blocks from the shapefiles without clear and obvious significant changes. (2) If I did redraw borders for survey block shape files, I used the following features as my guides for the new borders, knowing that surveys were most often carried out via vehicle. These features are ordered from highest priority guide to lowest: (i) Major roads that appeared to follow the shape of the survey block as shown in figures (ii) Major geographical features (e.g. bodies of water) that appeared to follow the shape of the survey block as shown in wolf report figures (iii) County lines (iv) When no obvious features were present, I used my best judgement to draw the new county lines (v) In all cases, I erred on simpler geometry rather than more complex geometry. While these decisions necessarily include a degree of subjective uncertainty on my part, I made them as conservatively as possible, and a priori of any statistical analysis of the data, so that any errors I made would be unbiased relative to the parameters of interest.

Table A1: Description of the changes made to Wisconsin DNR GIS files of Winter Survey Blocks to match maps in older Wisconsin DNR wolf population reports. All changes are described in reverse chronological order, as the changes were made relative to more contemporary maps. A change made for a given winter applies to all preceding winters as well, unless otherwise specified.

WINTER	BLOCK(S)	DESCRIPTION OF CHANGE
2010-11	117	Split at US Highway 12 and Sterling Avenue
	118	Split at Count Road 6 and at US Highway 10 (Not split at bulb on east because of a lack of any guiding feature, and the possibility that it was a visual artifact not caught in the old map figure')
	131	Extended to State Highway 29, State Highway 160, N Brown County Line Road, and Lake Michigan
	96	Split into Block 96 and Block 97 at Route 70
	68	Extended to Route 51 and Canadian NTC Railway
	69	Extended to Route 51, Canadian NTC Railway, WI River, Eggert Drive, Rock Falls Drive, JJ, Winkleman Ave and Nelson Ave
	70	Extended till Route 51
	71	Trimmed at County Road 6
	103	Extended to Johnson Falls Road and Bushman Road
	123	Trimmed at US Highway 90, extended till US Highway 94, added in area of Block labeled 223
	125,127,128,129	Did NOT change border between blocks 125 and 127 and between 128 and 129; shape of border irrelevant as it is within Petenwell lake either way
2009-10	70,71,72	Redrew borders to follow County Road K and Country Road G
	126	Trimmed at County Highway E and County Highway Z and N Riverside Drive
	41	Trimmed at Tuscobia State Trail, expanding Block 42
	89	Extended to Country Road F and County Road S and 5th Avenue
	20	Kept as 20A and 20B
	134	Border redrawn with N Division Street
	136	Drawn by negative space in file
	117	Trimmed at County Road M
	19	Extended into 20B with borders of 27th Street, 23rd Avenue, 20 ¼ s Street, and W Knapp St
2005-06	7	Extended via E County Road C, S County Road A and Tower Ave, removing from Block 5
	113	Split at County Road G, Country Road West, and Loomis Road into Block 113 and 114

B: Wolf Count Uncertainties

I treated WI DNR Wolf reported uncertainty by multiple imputation of reported ranges, where if a tracker reported an estimate of wolf counts between X and Y wolves in a given block, I used multiple imputed data sets drawing from a uniform distribution of integer wolf numbers between X and Y. I tested for asymptotic model results when deciding on the number of imputed data sets.

WI DNR Wolf reports presented wolf counts in a given survey block by a given tracker in several ways, which were treated differently for analysis. I treated a single number at face value (e.g. for 5 reported wolves, I use 5 wolves as the count). I treated a reported range as the bounds of a uniform distribution to draw from when generating imputed datasets (e.g. for 3-5 reported wolves, I draw an integer value from a uniform distribution between 3 and 5 to generate the wolf number for a single imputed dataset). For a number treated as a question mark, I did one of two things. In my default analyses, I only used the preceding number (e.g. 2? wolves is treated as 2 wolves), which is supported by the aggregated wolf counts from the winter track surveys, which treat these question marks the same way. I also tested including additional uncertainty by adding 1-wolf uncertainty (e.g. 3? wolves is treated as a uniform distribution from 2-4 wolves, 0? wolves is treated as a uniform distribution from 0-1 wolves as wolf numbers are of course bounded at 0). In some instances, the reported number was a dash mark (-) as opposed to 0 wolves. Without clarity on what this meant, I once again treated it as a 0 in the default analyses, and tested whether imposing a 0-1 uniform distribution on these reported numbers affected the analyses. Ultimately I did not find adding additional uncertainty of wolf numbers reported with question marks and dashes changed the analysis in any substantive way, so I ignored these symbols; this choice is supported by the DNR's aggregated wolf track survey totals.

C: Model Diagnostic and Summary Plots for Final Wolf Model

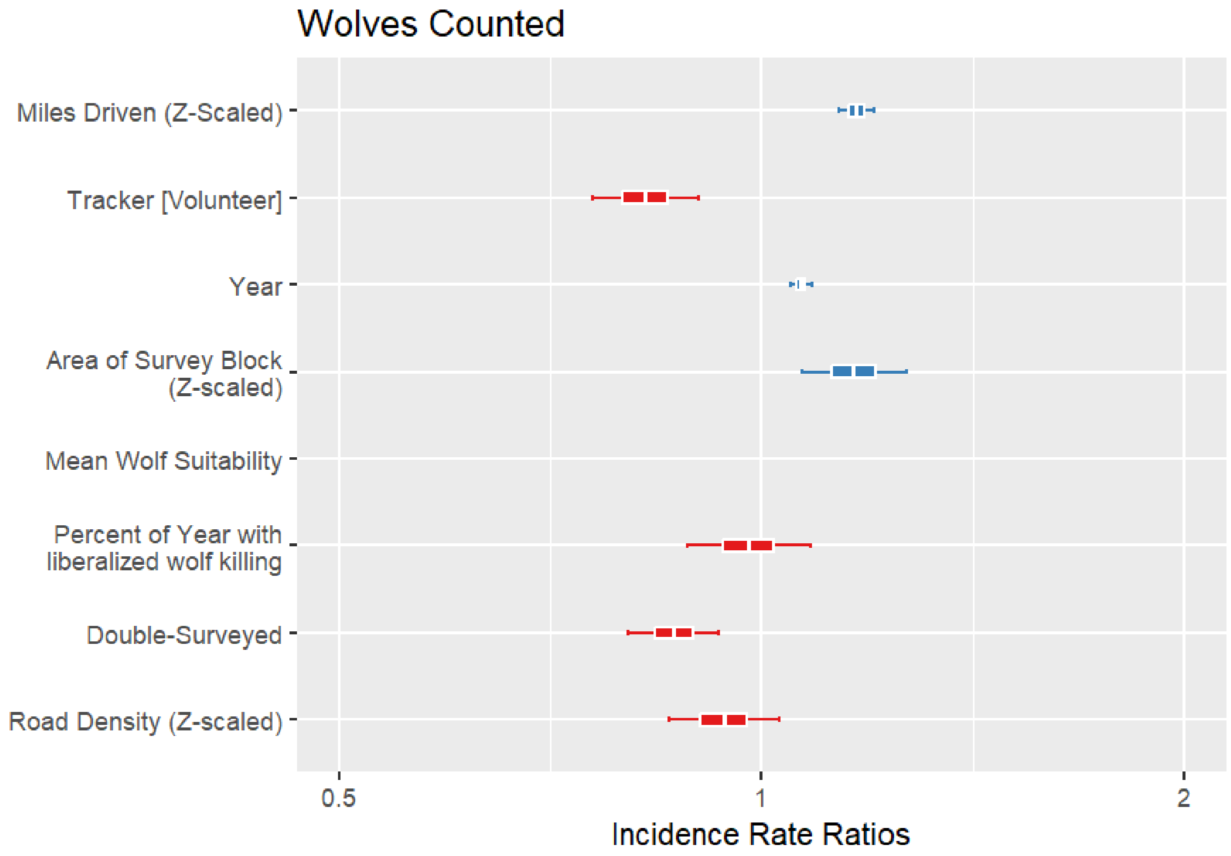


Figure A1: Wolf winter track survey (2003-11) Bayesian mixed effect model coefficients (transformed to Incidence Rate Ratios); Family=Hurdle Negative Binomial, Bars are 95% credible intervals. Plot truncated to show most fixed effects, so Mean Wolf Suitability is off axis, 95% CI=[1.92,6.92]. Results are shown for 1 of 3 imputed submodels, other submodels show similar results.

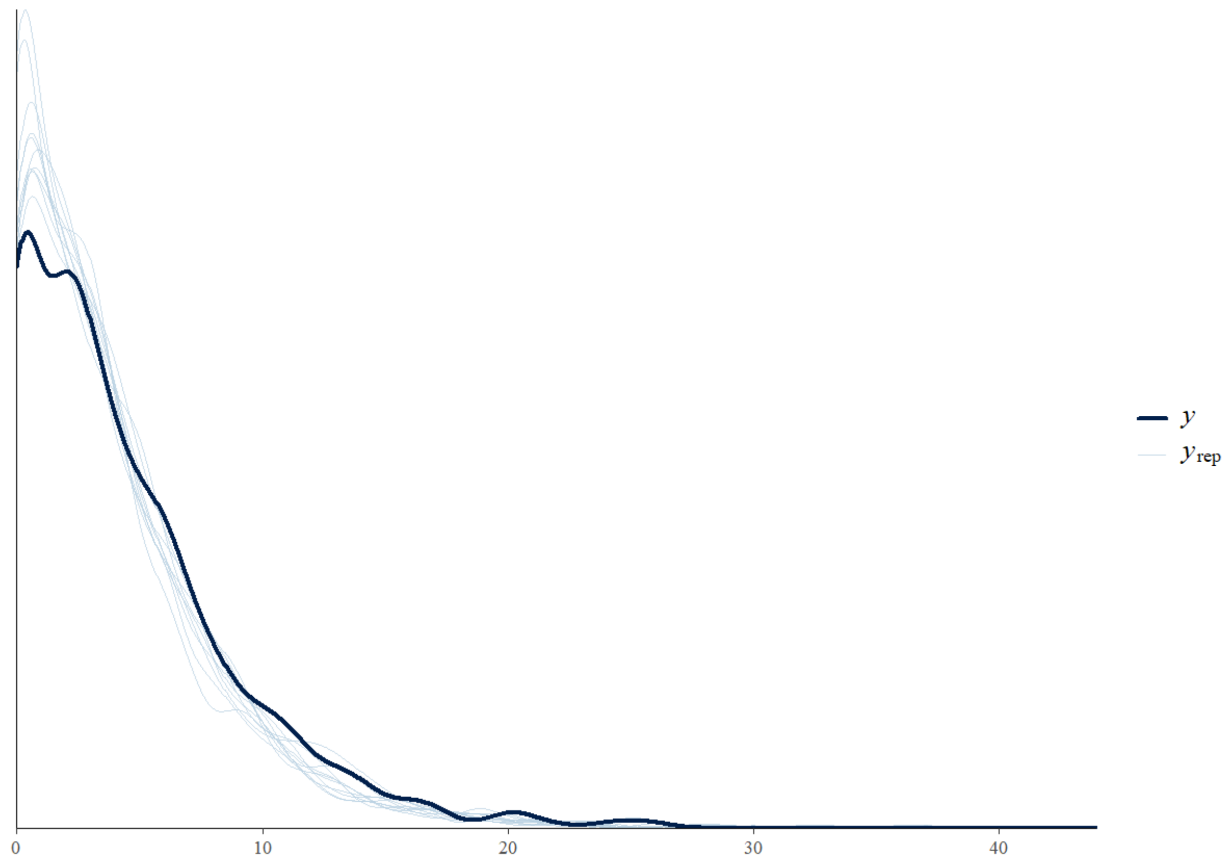


Figure A2: Wolf winter track survey (2003-11) Bayesian mixed effect model posterior predictive check (PPC). Imputed wolf numbers from one imputed set (of 3) plotted in black, simulated wolf numbers show in light blue; the y-axis shows frequency. Note the discrepancies in most simulations for wolf numbers below 5; the final model shown here minimized this artifact, while failing to eliminate it entirely. Results are shown for 1 of 3 imputed submodels, other submodels show similar results.

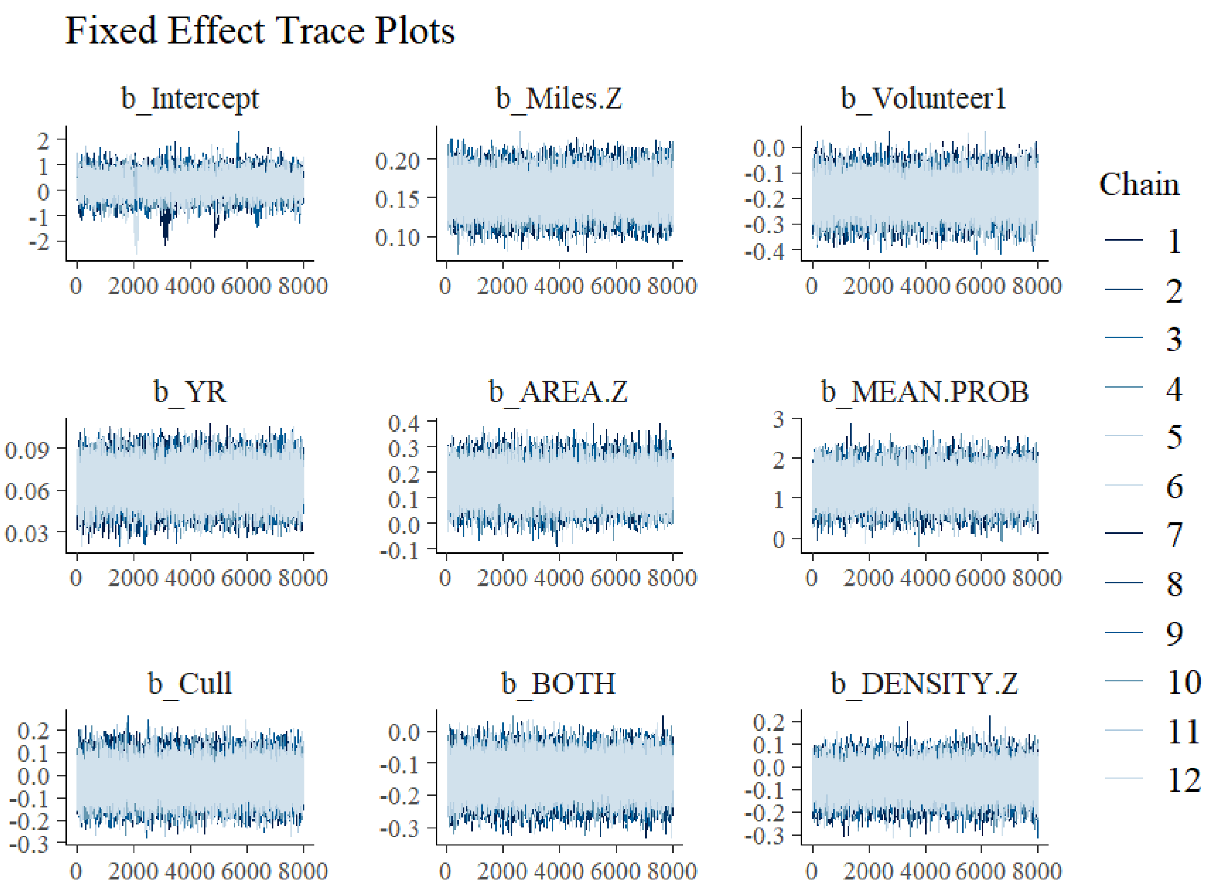


Figure A3: Wolf winter track survey (2003-11) Bayesian mixed effect model trace plots for fixed effects. The final model was run for 16000 iterations (8000 warmup) with 12 chains total (4 per imputed submodel, 3 imputed submodels included).

D: Simulation Marginal Distributions

To simulate wolf counts by Volunteers and DNR trackers with and without adjusted miles, I adjusted ‘missing’ wolf counts by tracker identity and miles driven with the following distributions (simulated across 1000 iterations). I derived gamma distributions for the effects of volunteer identity and (z-scaled) miles driven on wolf count by fitting gamma distributions to posterior estimates of coefficient mean and 95% CI for each parameter

$$Volunteer\ Marginal\ Effect \sim \Gamma(340.1975, 0.00244)$$

$$Miles.Z\ Marginal\ Effect \sim \Gamma(2704, 0.000433)$$

I plotted a histogram of the ratio of volunteer miles driven to DNR miles driven for double-surveyed blocks and tested the distribution to normal, lognormal, and gamma distributions. I found strongest AIC support for the lognormal distribution.

$$\frac{Volunteer\ Miles\ Driven}{DNR\ Miles\ Driven} \sim Lognormal(0.3696, 1.283)$$

Appendix 2

Table A1: Audio exemplar sources used for treatment and control playback experiments studying Amur tiger (*Panthera tigris*) nonlethal effects on ungulate prey in Sikhote Alin Biosphere Zapovednik in 2020 and 2021-22

Species	**Source**	**Catalog Number/URL**	**Recordist**
Tiger (*Panthera tigris*)	YouTube	https://www.youtube.com/watch?v=nJkAX5Q6Tj0	User @daesmae on YouTube
Tiger (*Panthera tigris*)	Berlin Natural History Museum, Animal Sound Archive	Panthera_tigris_V_2076_20_2	Günter Tembrock
Tiger (*Panthera tigris*)	Berlin Natural History Museum, Animal Sound Archive	Panthera_tigris_V1502_48	Günter Tembrock
Red fox (*Vulpes vulpes*)	Macaulay Library, Cornell Lab of Ornithology	60082	William Seward
Red fox (*Vulpes vulpes*)	Macaulay Library, Cornell Lab of Ornithology	71612	Arnoud B. van den Berg

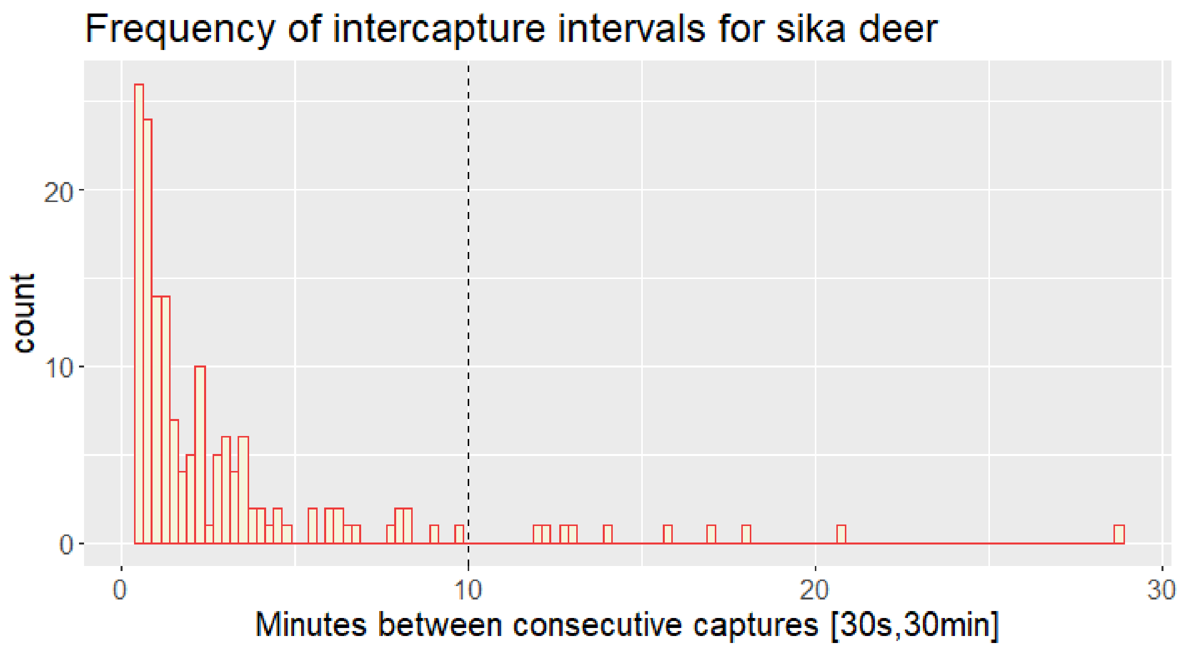


Figure A1: Sika deer (*Cervus nippon*) intercapture interval for photocaptures between 30s and 30 min in Sikhote-Alin Biosphere Zapovednik 2019-2022

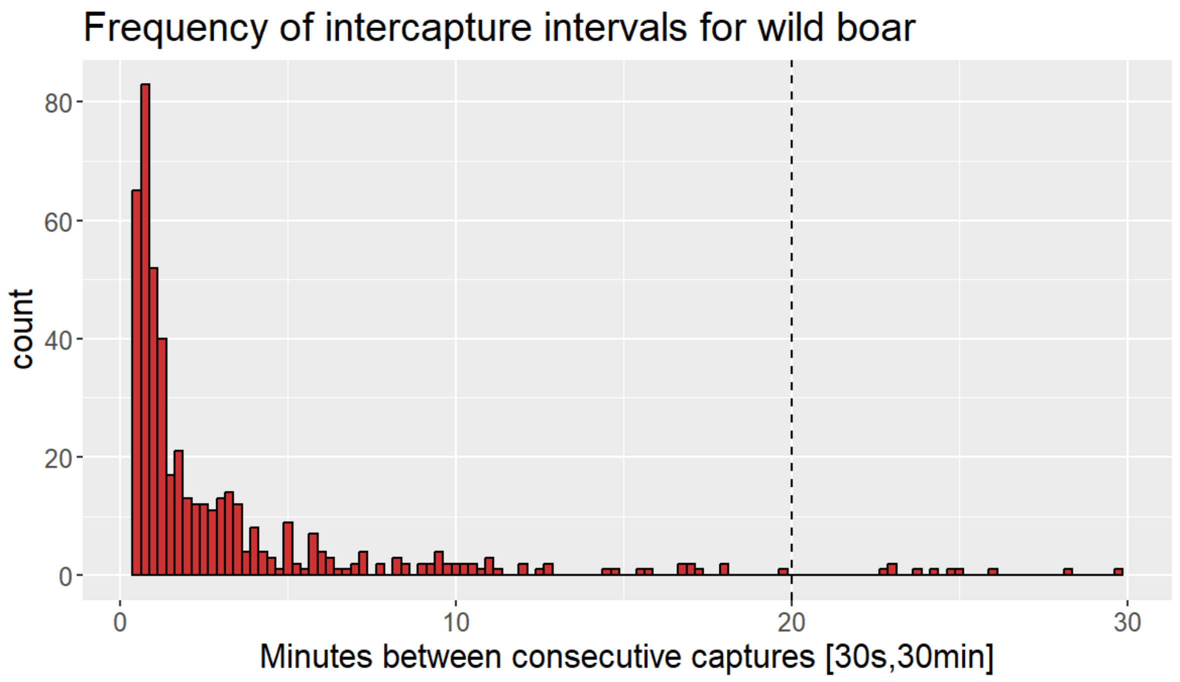


Figure A2: Wild boar (*Sus scrofa*) intercapture interval for captures between 30s and 30 min in Sikhote-Alin Biosphere Zapovednik 2019-2022

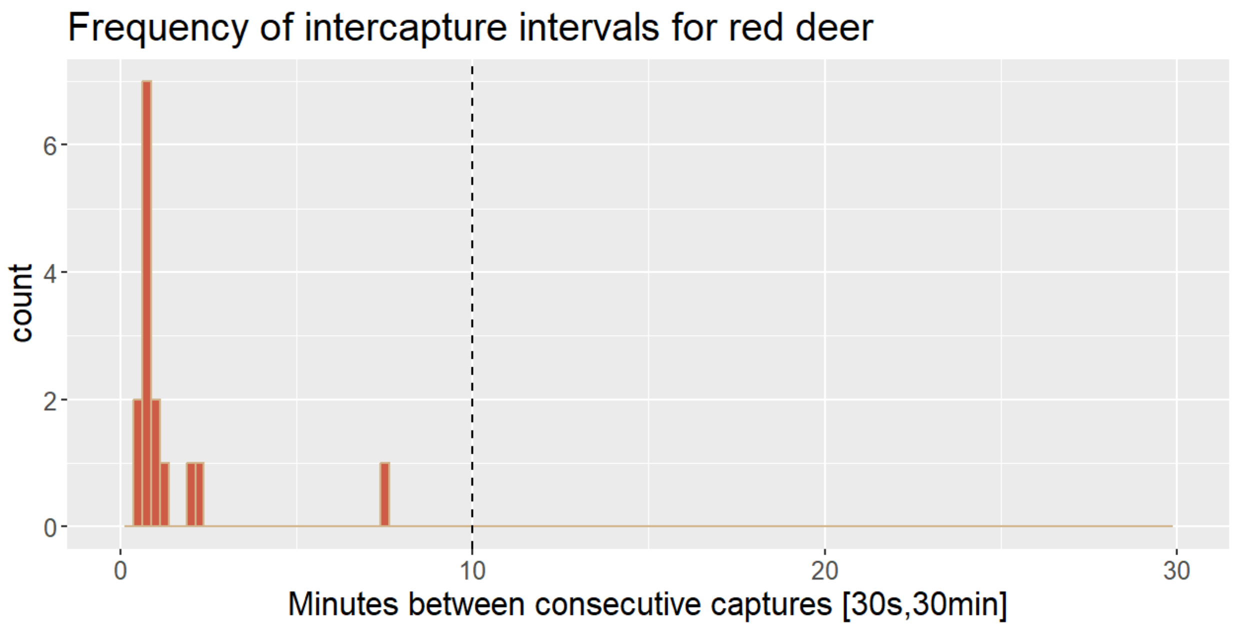


Figure A3: Red deer (*Cervus canadensis*) intercapture interval for captures between 30s and 30 min in Sikhote-Alin Biosphere Zapovednik 2019-2022

Appendix 3

A: LotL+KP Prey Indexing

Kerley et al 2015 only reported relative abundances of primary ungulate prey species (wild boar, sika deer, and roe deer) in their study sites, including LotL+KP (104). I came up with relative (individual) abundances of 75%, 12.5% and 12.5% for sika deer, wild boar, and roe deer respectively (104). To derive an ecologically reasonable estimate of ungulate biomass from these relative abundances, I chose to assume that one of those prey species occurred at similar individual densities as in SABZ, and used that as an index to estimate biomass of the other two species. Using wild boar as the index, I arrived at an average prey biomass in LotL of 1808 kg/km^2, which is an order of magnitude above reported total prey biomass in other Amur tiger sites and thus biologically unreasonable (161). Using sika deer and roe deer as the index, I arrived at much more reasonable biomass estimates of 90.4 kg/km^2 and 113 kg/km^2 respectively. I decided to use roe deer as an index, as it yielded the median prey biomass estimate among all three, and because assuming a higher biomass of deer reinforces these models as best case scenario simulations for tigers in and around protected areas.

B: Carrying Capacity Figures

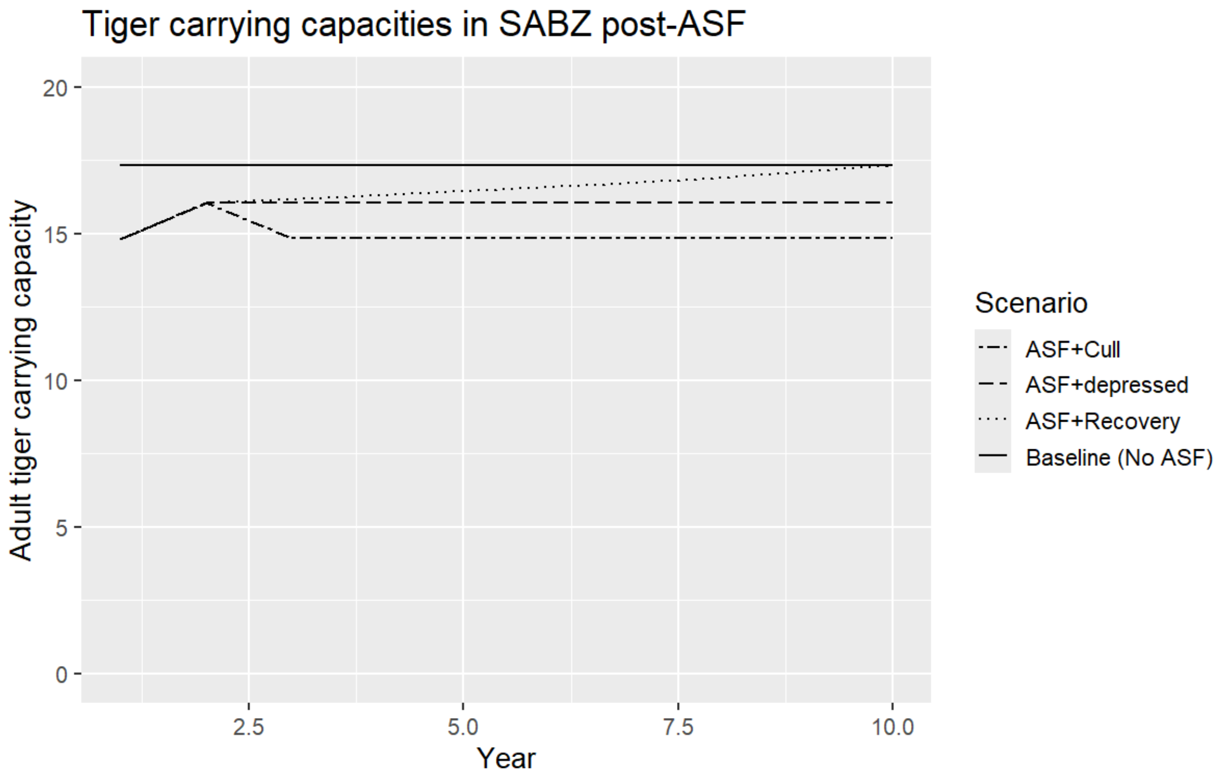


Figure A1: Changes in adult Amur tiger carrying capacity in Sikhote-Alin Biosphere Zapovednik (SABZ) under different African Swine Fever (ASF) scenarios. Baseline: no ASF; ASF+Recovery: wild boar densities steadily recover after the first two years of ASF; ASF+depressed: Wild boar densities remain persistently low after the first two years of African Swine Fever; ASF+Cull: Wildlife management culls wild boar to keep them below a threshold where they will continue to spread ASF.

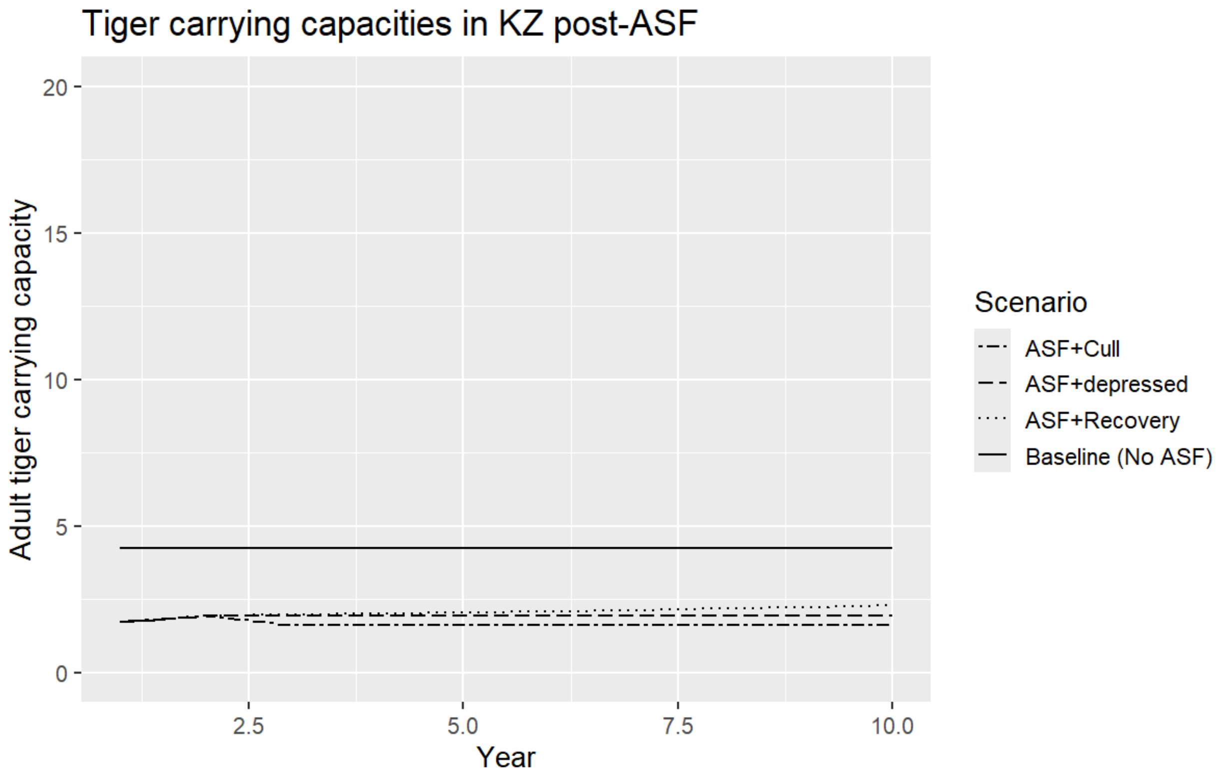


Figure A2: Changes in adult Amur tiger carrying capacity in Khinganskiy Zapovednik (KZ) under different African Swine Fever (ASF) scenarios. Baseline: no ASF; ASF+Recovery: wild boar densities steadily recover after the first two years of ASF; ASF+depressed: Wild boar densities remain persistently low after the first two years of African Swine Fever; ASF+Cull: Wildlife management culls wild boar to keep them below a threshold where they will continue to spread ASF.

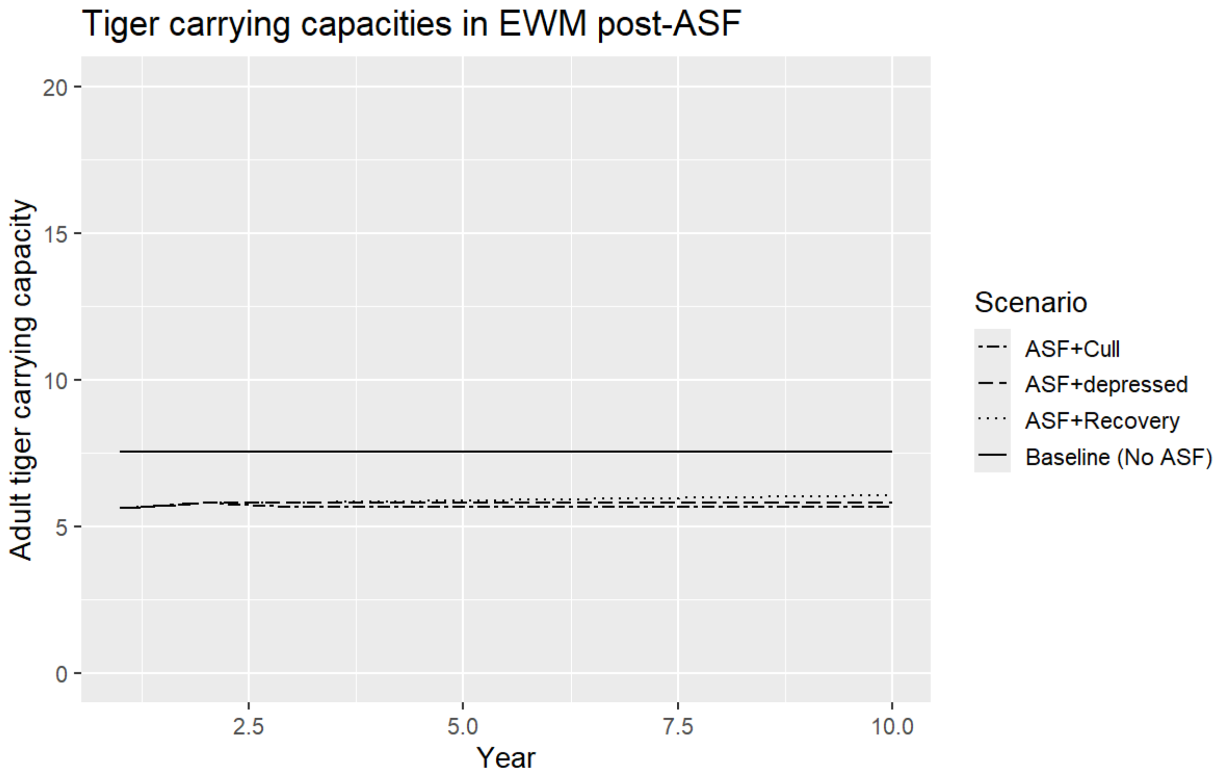


Figure A3: Changes in adult Amur tiger carrying capacity in the Eastern Wanda Mountains (EWM) under different African Swine Fever (ASF) scenarios. Baseline: no ASF; ASF+Recovery: wild boar densities steadily recover after the first two years of ASF; ASF+depressed: Wild boar densities remain persistently low after the first two years of African Swine Fever; ASF+Cull: Wildlife management culls wild boar to keep them below a threshold where they will continue to spread ASF.

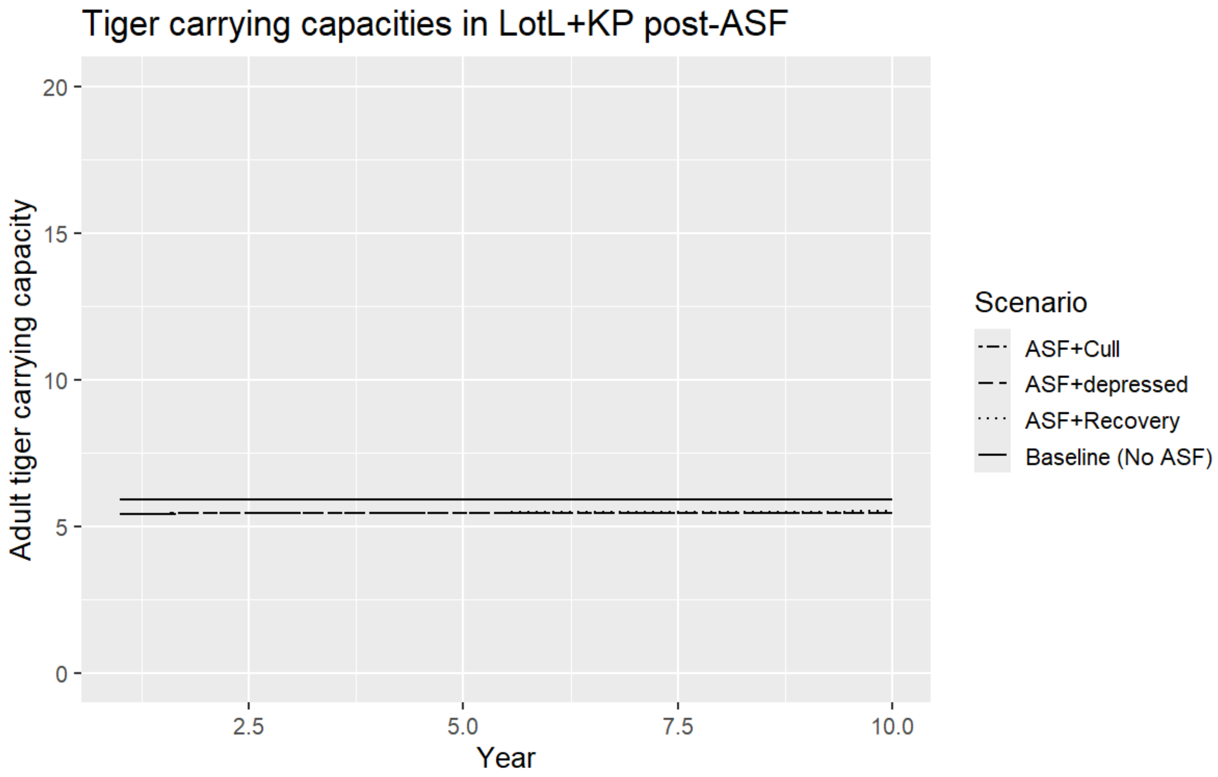


Figure A4: Changes in adult Amur tiger (*Panthera tigris*) carrying capacity in Land of the Leopard and Kedrovaya Pad (LotL+KP) under different African Swine Fever (ASF) scenarios. Baseline: no ASF; ASF+Recovery: wild boar densities steadily recover after the first two years of ASF; ASF+depressed: Wild boar densities remain persistently low after the first two years of African Swine Fever; ASF+Cull: Wildlife management culls wild boar to keep them below a threshold where they will continue to spread ASF.

C: Truncated Quasi-Extinction Probability Figures

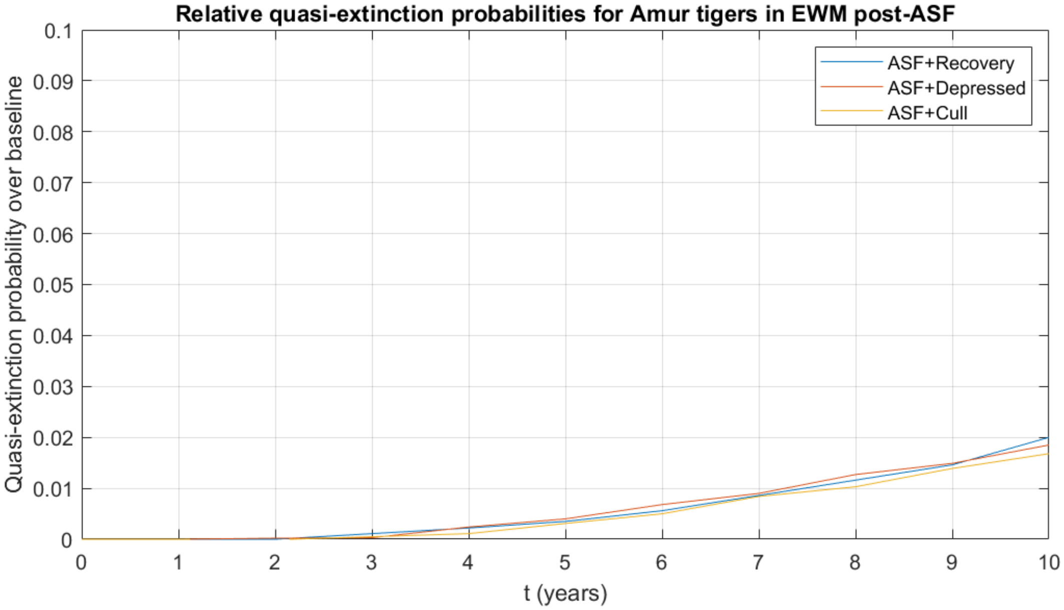


Figure A5: Relative quasi-extinction probability for Amur tigers (*Panthera tigris*) in the Eastern Wanda Mountains (EWM) under different African Swine Fever (ASF) scenarios. All scenarios are plotted as the additional quasi-extinction probability relative to the baseline scenario of no ASF. Truncated to more clearly show the additional effect of different ASF simulations versus baseline.

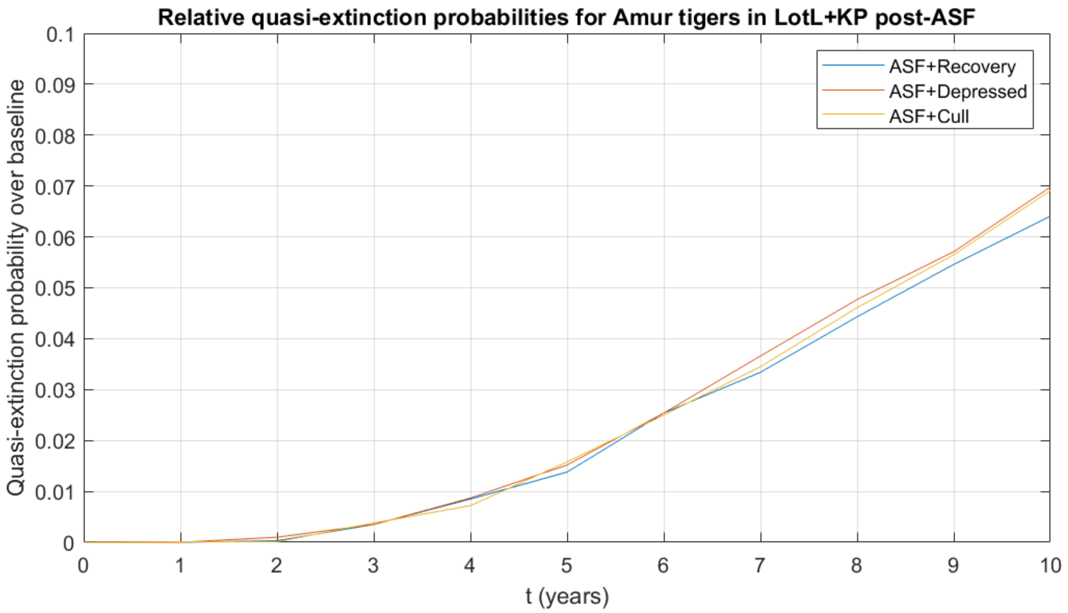


Figure A6: Relative quasi-extinction probability for Amur tigers (*Panthera tigris*) in Land of the Leopard and Kedrovaya Pad (LotL+KP) under different African Swine Fever (ASF) scenarios. All scenarios are plotted as the additional quasi-extinction probability relative to the baseline scenario of no ASF. Truncated to more clearly show additional effect of different ASF scenarios versus baseline.

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