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Vigilance of Plains Bison (Bison Bison Bison) does not vary with Human Hunting Pressure: The Influence of Constitutive Defenses

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Abstract

Where large carnivores are absent it is frequently claimed that human hunters are their fitting surrogates. If human hunters are functionally equivalent to large carnivores, then species that are hunted by these two predators should fear both equally. Yet, ungulates can show stronger behavioral responses to human predators than to predation risk posed by large carnivores. Vigilance – the interruption of some behavior to visually survey surroundings - is generally elevated in wildlife populations that are hunted by humans. However, do species with strong constitutive defenses (e.g., large and hard to kill) adjust their vigilance in areas where they are hunted by humans? Behavioral and ecological responses by plains bison (Bison bison bison) – species with strong constitutive defenses - in populations subjected to human hunting will be crucial to their successful restoration and long-term conservation. Therefore, we investigated the relationship between human hunting and vigilance across 12 bison populations exposed to different levels of hunting. The average proportion of adult bison vigilant in hunted and non-hunted populations was similar. Furthermore, vigilance did not vary based on hunting frequency, recent hunting history, or group size. While sample size is low, our data also indicate that vigilance is essentially equal between populations hunted solely by humans and populations without human hunting but with large carnivores (wolves and grizzly bears). Aside from the differential influences on population size and demography, predation by humans and large predators appears to be functionally redundant with respect to vigilance in the populations that we have observed.

Keywords: Carnivores; Smaller-Bodied Mammals; Haphazard; Bison; Vigilance

Abbreviations: CSP: Custer State Park; BNP: Badlands National Park; PRR: Pine Ridge Reservation; SGLU: Sinte Gleska University; LBR-BGU: Lower Brule Reservation Big Game Unit; CRU: Cherry Ranch Unit; HRU: Huston Ranch Unit; FLY-D: Flying D Ranch; OSPRA: Oglala Sioux Parks and Recreation Association; OLC: Oglala Lakota College

Introduction

Where large carnivores are absent it is frequently claimed that human hunters are fitting surrogates for natural predators Berger [1], Clinchy [2] that is, human hunting exerts the same influence on prey (i.e., are functionally equivalent) as their non-human predators. If so, then species that are hunted by both native carnivores and humans should fear both equally. Yet, ungulates can show stronger behavioral responses to human predators than to predation risk posed by large carnivores Proffitt [3], Ciuti [4]. Since human hunting is a form of predation risk it can divert time/energy from fitness-enhancing activities like feeding, parental care, mating Lima & Dill [5], Lima [6] and predator avoidance. Habitat selection, group size, and flight initiation distance are also impacted by predation risk Anholt & Werner [7], Dill [8], Lima & Dill [5], Turner [9], Vos [10]; Ydenberg & Dill [11], Stankowich [12]. Vigilance – the interruption of some behavior to visually survey surroundings Quenette [13] – is generally elevated in wildlife populations that are hunted by humans. Red deer (Cervus elaphus), roe deer (Cervus capreolus), impala (Aepyceros melampus), Mediterranean mouflon (Ovis gmelini musimonxOvis sp.), Fallow Deer (Dama dama) Blue Sheep (Bharal: Pseudois nayaur), and wild boar (Sus scrofa) all demonstrate increased vigilance in areas hunted by humans Matson [14], Benhaiem [15], Benoist [16], Jayakody [17], Pecorella [18], Podgórski [19], Kandel [20]. Vigilance time of impalas was also longer on a property where they were hunted by humans more frequently than on an adjacent property with reduced hunting Matson [14]. Therefore, vigilance can be positively associated with the intensity (e.g., frequency, # of hunters, # of animals taken) of human hunting.

Because ungulates can show stronger behavioral responses to human predators than to predation risk posed by large carnivores Proffitt [3], Ciuti [4], inducible defenses- (i.e., responses activated through a previous encounter with a predator that confer improved ability to thwart subsequent attacks), like vigilance, may be strongest when humans behave as functional predators Clinchy [2], Ordiz [21], Palumbi [22]. Increased vigilance in ungulates appears to be universally associated with human hunting and can be costly Matson [14], Benhaiem [15], Benoist [16], Jayakody [17], Podgórski [19]. Decreased fitness can occur via escalation of physiological stress Arlettaz [23], and in some cases, human-induced stress has been linked to lower reproductive output Pauli and Buskirk [24], French [25] and reduced offspring survival Mann [26], Phillips and Alldredge [27]. However, does vigilance in species with strong constitutive (e.g., large and hard to kill) defenses also increase in areas where they are hunted by humans? This gap in the literature is particularly relevant to plains bison (Bison bison bison) – a species with strong constitutive defenses – especially in light of the widespread hunting of them for meat and trophies. Population-level responses of bison to human hunting will be crucial to their successful restoration and long-term conservation. Therefore, it is important that we understand the degree to which human hunting influences bison behavior.

Sarno [28] previously reported a negative association between hunting and male vocal advertisement during the reproductive season in plains bison. Since the mating behavior of bulls may be disrupted by hunting, a logical prediction is that bison increase their vigilance in areas where they are hunted by humans. Bison vigilance is lower than that of other smaller-bodied mammals with whom they overlap spatially and temporally Berger and Cunningham [29], Borkowski [30], Creel [31], Laundré [32], Hernández and Laundré [33]. But, how will they react to the presence of human predators? Therefore, our primary objective was to use scan-sampling to compare vigilance of bison in protected and hunted populations. We predict that bison – having strong constitutive defenses – will not adjust their vigilance to human predators; bison in hunted and non-hunted populations will exhibit similar levels of vigilance. Furthermore, we predict that hunting pressure (measured as the number of hunt months/year and recent hunting history) will not be associated with bison vigilance. Plains bison exhibit a definable herd structure in which cows, calves, and immature males form somewhat transient mixed-sex and age groups. Mature bulls form smaller all-male groups or remain solitary for much of the year Berger and Cunningham [34]. During the breeding season (rut) bison form large aggregations where mature bulls join mixed-sex and age groups. Males exhibit a linear dominance hierarchy, whereby larger, mature bulls are dominant to smaller, younger bulls Roden [35]. Dominant males temporarily consort with cows prior to or during estrus and attempt to keep all other bulls away by engaging in vocalizations, threat displays, and fights Berger and Cunningham [34] RJ Sarno pers obs.

Methods

Study Sites

Data were collected from 12 study sites in South Dakota, North Dakota, and Montana. South Dakota study sites included Wind Cave National Park (WICA) (43.5724°N, 103.4416°W), Custer State Park (CSP) (43.7638°N, 103.3703°W), Badlands National Park (BNP) (43.8554°N, 102.3397°W), Pine Ridge Reservation (PRR) (43.2731°N, 102.7445°W), Rosebud Sioux Indian Reservation-Sinte Gleska University (SGLU) (43.187505°N, 100.6257°W), and three pastures on the Lower Brule Reservation Big Game Unit (LBR-BGU) Cherry Ranch Unit (LBR-CRU), and Huston Ranch Unit (LBR-HRU) (44.08°N, 99.78°W). The Standing Rock Indian Reservation (2 pastures SRN, SRS) (46.0869°N, 100.6301°W) and Theodore Roosevelt National Park (46°58'N, 103°27'W) were located in North Dakota. The Flying D Ranch (FLY-D) (45.4991°N, 111.3194°W) was located in Montana. The study areas varied in elevation from 498 to 1612 m. All study populations were located within the mixed-grass prairie ecoregion. While study sites were relatively level, the landscape was undulating and at times bisected by steeply-sloped drainages. Common grasses include little bluestem (Schizachyrium scoparium), blue grama (Bouteloua gracilis), big bluestem (Andropogon gerardii), western wheatgrass (Pascopyrum smithii Rydb.), buffalograss (Buchloe dactyloides), cheat grass (Bromus tectorum), and needle-and-thread grass (Stipa comata). Rocky Mountain juniper (Juniperus scopulorum), green ash (Fraxinus pennsylvanica), eastern cottonwood (Populus deltoides), Ponderosa pine (Pinus ponderosa), and white spruce (Picea glauca) were the most common forest types, and dominated the drier slopes, butte edges, and upper draws of the study areas National Park Service [36], South Dakota Game Fish, and Parks [37], Graham and Gingerich [38], Suttie [39]. All study sites occurred within a semiarid climatic zone. Average yearly precipitation varied from 400mm (Badlands National Park, SD) to > 960 mm (FLY-D, MT), and most occurred between April and September. Mean yearly temperatures varied from a low of 6.1 ^{o}C (FLY-D) to a high of 10.7 ^{o}C (Custer State Park)

Hunting

Bison were hunted 0 months/year (BNP, TRNP, WICA), > 0 months but < 1 month SRR-W, 2 months/year (FLY-D), 3 months/year (SRR-N), 4 months/year (CSP, LBR –BGU, LBR-CRU), 5 months/year (LBR-HRU), and 12 months/year (SGU, PRR). Bison hunts generally lasted 1-2 hours. Hunting parties were

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mostly comprised of 1 guide, 1 hunter, and 1-2 of the hunter's companions and/or the guide's assistant. Targeted bison were usually approached by 1-2 motor vehicles to within 50-100m. Hunters utilized .270 or .25-06 caliber centrefire rifles and generally removed non-lactating cows, 2-3 year old bulls, and older bulls. On PRR there were also commercial hunts whereby up to eight animals were removed over a 6 h period. Bison were first driven into a holding corral where two people approached bison to within 25-50 m before discharging their rifles. One animal at a time was downed and carcasses were removed from the pasture and processed at which time shooters re-entered the pasture and repeated the procedure (53). Remaining animals were then re-released into the pasture (T Ecoffey, United States Department of Agriculture, pers. comm., 2014).

Data Collection

Vigilance was defined as an adult bison with its head at or above shoulder level while stationary. Adults were defined as animals greater than 1 year old (when marked) or by body size when not marked. We measured the proportion of adults in a group that were vigilant. At 1-minute intervals scans were performed from left to right and the number of animals vigilant and not vigilant were counted. Observations were collected during the rut (July/August). We observed a total of 325 groups in 2018-2021. Observations were conducted on 66 groups in BNP, 20 groups in Custer State Park, 75 groups on FLY-D Ranch, 30 groups on Pine Ridge Reservation, 14 groups from the SGU herd (Rosebud Reservation), 19 groups on the Lower Brule Reservation - 6 groups from BGU, 5 groups from CRU, and 8 from HRU. A total of 29 groups on Standing Rock Reservation - 22 groups from SRR-N, and 7 groups from SRR-W, 32 groups in TRNP, and 21 groups from WICA. Group size and composition were defined by the number of animals within 50 m of each other Sarno [28]. We attempted to minimize pseudo-replication by identifying adults based on tag numbers and/or natural markings. When adults could not be distinguished by natural markings or ear tags, we visited different groups for each observation and focal individuals were selected haphazardly. We observed bison as close as we could safely approach them throughout the day (50 m), while attempting to avoid oversampling during any particular time of day. Bison did not appear to be bothered by the presence of our vehicle in any of the study sites as cows and calves routinely passed within 3 m of our parked vehicle. Bulls also passed by our parked vehicle within 3-5 m while bellowing and fighting other bulls as well as accompanying cows. Therefore, we do not believe that the data were influenced by our presence Sarno [28].

Ethics Statement

Bison were observed only in areas where they were subjected to regular human visitation. Data collection did not involve restricted habitat or interference with other species, and was in compliance with institutional (Hofstra University IACUC # 16/17-13) and national guidelines for ethical conduct in the care and use of nonhuman animals in research. We obtained permission to conduct fieldwork in all study locations.

Data and Variables Description

For statistical modelling purposes we defined our group-level response variable, Vigilance (i.e., Average Proportion Heads Up), and our location-level predictor variables: Hunting Status, Recent Hunting History, Number of Hunt Months and Average Group Size. Because of animals leaving the area and/or being obscured during observations, the number of scan-sampling periods varied between 5 and 10 depending on the group. We expressed the proportion of bison vigilant in each scan as the number of adult bison holding their head up out of all adult bison observed during that observation. For each group of bison in our study, we obtained a single value for this response variable. In (Table 1) we illustrate how we calculated the average vigilance for a group of size 12, containing 11 adult bison whose vigilant behavior was observed for 10 minutes. Location-level predictor variables were defined as follows. Hunting Status was designated as a binary variable taking the values 1 for a hunted population and 0 for a non-hunted population. Recent Hunting History was defined as a categorical variable with categories labeled as Never, Current Month, 4.5 Months Prior to Current Month, and 7+ Months Prior to Current Month. Number of Hunt Months was defined as a categorical variable with 3 categories: 0 Months, 6 Months or Less, and 12 Months. Average group size was calculated as the average size of all groups within a population. Five combinations of location-level predictor variables were represented in the data, therefore we used these combinations to create five distinct hunting profiles (Table 2). Each of these hunting profiles corresponds to a distinct bison population.

Statistical Methodology

Our statistical modelling was driven by our specific research hypotheses. To reflect this, we did not formulate multiple competing models with the aim of comparing them based on an information criterion such as AIC to choose a "best" model Burnham and Anderson [40]; instead, we formulated a single model which enabled us to test all of our research hypotheses simultaneously. Our proposed model captured the following study design and data aspects: 1) the boundedness of the values of the response variable (Average Vigilance) between 0 and 1; 2) each value of the response variable was expressed as an average proportion over a certain number of 1-minute scan samples; 3) the variation in the number of 1-minute observation periods across groups that varied between 5 and 10; and 4) the nesting of bison groups within locations. To address items 1 and 2, we used an ordered beta regression model Kubinec [41]. This type of model can accommodate response variables whose values are bounded in the range 0 to 1 and can easily handle situations where a non-negligible proportion of these values would equal 0

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and/or 1. To address item 3), we included response weights in the model that were proportional to the number of 1-minute intervals used in the derivation of the response value for each bison group. This way, response values obtained from a larger number of such intervals (e.g., 10 1-minute intervals) could receive more weight in the model compared to response values obtained from a smaller number of such intervals (e.g., 5 1-minute intervals). To address item 4), we included a random effect of location in our model; its inclusion allowed us to account for the potential correlation among response values coming from bison groups observed at the same location.

Table 1: Calculation of average proportion of bison vigilant in a population with 11 adults.

Group #	Observation #	# Adults	# Bison with Heads Up	Proportion Bison with Heads Up
2	1	11		2/11 = 0.18
2	2	11	2	6/11 = 0.55
2	3	11	68	8/11 = 0.73
2	4	11	9	9/11 = 0.82
2	5	11	6	6/11 = 0.55
2	6	11	5	5/11 = 0.45
2	7	11	1	1/11 = 0.09
2	8	11	0	0/11 = 0.00
2	9	11	1	1/11 = 0.09
2	10	11	1	1/11 = 0.09

Average Proportion Heads Up = (0.18 + 0.55 + 0.73 + 0.82 + 0.55 + 0.45 + 0.09 + 0.00 + 0.09 + 0.09_/10 = 0.36.

Table 2: Hunting profiles for 12 bison populations in our study in South Dakota, North Dakota, and Montana from 2018-2021.

Hunting Profile	Hunting Status	Recent Hunting History	# Hunt Months	Location
# 1	No	Never	0 Months	BNP, TRNP, WICA
# 2	Yes	4.5 months prior to current month	< 6 Months	CSP, LBR-BGU, LBR-CRU, LBR-HRU
# 3	Yes	Current Month	< 6 Months	SRR-N, SRR-W
# 4	Yes	Current Month	12 Months	FLY-D
# 5	Yes	7+ Months prior to current month	< 6 Months	PR-YB, SGU-S

Because our ordered beta regression model included a random effect of location, it can be thought of as a mixed-effects model. We fitted it to our data using the Bayesian model-fitting package ordbetareg available in software R Core Team [42], Kubinec [43]. We used default weakly-informative priors. Prior to using the model for inference, we assessed it for convergence and validity. Convergence of the model was assessed to ensure that the algorithm used to fit the model found the optimal solution, yielding estimated values for the model parameters that are trustworthy and can be interpreted. We used both numeric and visual convergence diagnostics. Specifically, we checked the R ˆ values of the model parameter estimates. We interpreted (R) ˆvalues smaller than 1.01 for all these estimates to signify model convergence Vehtari [44]. Trace and density plots were also examined visually. We assessed the validity of the model via two posterior predictive checks. One check in which we did not distinguish by location and the other in which we did distinguish by location. These checks involved simulating 200 data sets from the fitted model and comparing the distributions of the simulated vigilance values against that of the observed vigilance values using density plots (i.e., smoothed versions of histograms). If the model converged and captured the data well, the density plots of vigilance in the simulated data sets would be roughly similar in shape to the density plot of vigilance in the actual data. The density plots of the simulated data would also contain the plot of the actual vigilance vales.

Once convergence and validity of the fitted model were established, we used the model to test the comparisons of interest to us among the bison populations included in this study. These comparisons (Table 3) involved the (overall) mean of the response variable (vigilance) among populations described by specific hunting profiles. The hunting profiles were chosen in such a way as to permit the estimation of the effect of Hunting Status, Recent Hunting History, and Number of Hunt Months on bison vigilance. Thus, comparing different groups amounted to testing whether the effect of our predictor variables on the (overall) mean value of vigilance was small enough to be considered negligible. We tested for equivalence encapsulated by each of the comparisons of interest using the concept of ROPE (i.e., Region of Practical Equivalence), that is, a region of basically no effect. The ROPE is defined a priori as a range of values symmetric about 0 that controls how small we consider the effect captured by a comparison to be for us to declare it negligible. We proceeded in slightly different ways depending on whether our comparisons were simple or complex. Simple comparisons contrasted a single bison population against another bison population (as is the case for comparisons 4 and 6, (Table 3). Complex comparisons contrasted multiple bison populations against a single bison population (as is the case for comparisons 1, 2, 3, 5 and 7, (Table 3). Below, we describe how we proceeded for the simple comparison 4 and the complex comparison 1, respectively. For comparison 4, we first used the fitted model to obtain the posterior distribution of mean vigilance for a typical population with hunting profile # 2 and a typical population with hunting profile # 5 (Table 2).

Table 3: Comparisons of interest among sets of bison populations based on their hunting profiles.

	Sets of Bison Populations		**Purpose of A vs B Comparison**
Comparison	A	B	Test the Practical Equivalence of the Effect of the Following
1	# 1	# 2, 3, 4, 5	Hunting Status No vs Yes
2	# 3, 4	# 2	Recent Hunting History Current Month vs 4.5 Months Prior to Current Month
3	# 3, 4	# 5	Recent Hunting History Current Month vs 7+ Months Prior to Current Month
4	# 2	# 5	Recent Hunting History 4.5 Months Prior to Current Month vs 7+ Months Prior to Current Month
5	# 1	# 2, 3, 5	Number of Hunt Months 0 Months vs < 6 Months
6	# 1	# 4	Number of Hunt Months 0 Months vs 12 Months
7	# 2, 3, 5	# 4	Number of Hunt Months < 6 Months vs 12 Months

Next, we obtained the difference of these posterior distributions and used it to construct an 89% and 95% Highest Density Interval (HDI) for the true difference in the two mean values. The HDI for a parameter is the Bayesian equivalent of a confidence interval. It is defined in relation to the posterior distribution of that parameter such that it contains credible values for that parameter; all the values contained inside this interval have higher credibility than any value outside the interval. The Bayesian literature suggests that the 89% HDI is computationally more stable than the 95% HDI, so we favored it Kruschke [45]. We only included the 95% HDI because the 95% confidence level is ubiquitous in frequentist statistics. Next, we committed to a pre-defined ROPE Radius of 0.20 for the true difference in mean values of vigilance across the two bison populations being compared. Given that others may be interested in a different value for the ROPE Radius, we also considered what would happen if we allowed the ROPE Radius to vary from 0.001 to 0.30 in steps of 0.001. Any particular ROPE Range, defined as (-ROPE Radius, +ROPE Radius), is intended to capture the range of values of the true difference in (overall) mean values of vigilance that one believes to be consistent with practically equivalent vigilance behavior between the two bison populations being compared. For the ROPE Radius of 0.20 that we committed to (ROPE Range of (-0.20, +0.20)), we plotted the 89% HDI and the 95% HDI against this range. We then used the ROPE + HDI Decision Rule to determine what percentage of the 89% HDI was found to fall inside the ROPE Range (similarly for the 95% HDI). If this percentage was 100%, we accepted the null hypothesis of equivalence in vigilance between the two populations being compared. If it was 0%, we rejected it. If it was > 0% and < 100%, we remained undecided.

Finally, we plotted the percentage of the 89% and 95% HDI intervals falling inside the ROPE as a function of the ROPE Radius and used that percentage to determine the minimum ROPE Radius beyond which the data would support equivalence. Equivalence was concluded when 100% of the HDI interval was inside the ROPE, as per the HDI + ROPE decision rule Kruschke [46], Kruschke and Liddell [47]. For comparison 1, we proceeded in a similar fashion, the only difference being that we started by obtaining the posterior distribution of the mean value of vigilance for a typical bison population with hunting profile # 1 and the overall mean values of vigilance across the four typical bison populations with hunting profiles # 2, # 3, # 4 and # 5. The overall mean vigilance was obtained as an unweighted average of the individual mean values of vigilance for the bison populations with hunting profiles # 2, # 3, # 4 and # 5. We reported the estimated marginal effect of average group size on vigilance in our model, along with an uncertainty interval that was computed as an 89%

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quantile credible interval. We calculated the estimated marginal effect of average group size as follows: First, we estimated mean vigilance for each bison group represented in our data by plugging into the model the observed values of the hunting-related predictors and the average group size for a given population. Second, we marginally increased average group size and repeated the calculation in step one with this slightly increased average group size. Third, for each bison group, we computed the change in the mean values of vigilance obtained in the first two steps. Forth, we averaged the changes in the third step across all bison groups. (Note that mean vigilance is on a 0 to 1 scale.)

Results

The average proportion of adult bison vigilant in hunted ($\bar{x}$=0.23) and non-hunted populations ($\bar{x}$=0.26) is similar (where $\bar{x}$ denotes a weighted mean). Both distributions display a sizeable amount of proportions equal to 0 (displayed via red vertical bars at the left end of the histograms) and a much smaller, yet non-negligible amount of proportions equal to 1 (displayed via red vertical bars at the right end of the histograms) (Figure 1). The 12 locations exhibited wide variation in the number of bison groups that we observed; we observed 5 groups for the LBR-CRU location and 75 for the FLY-D location. Weighted mean vigilance varied from 0.164 (SRR-N) to 0.468 (SGU-S) location (Figure 2). Weighted mean vigilance across sets of hunting profiles is similar both within and across sets of bison populations for all the comparisons of interest (Figure 3). The mixed effects ordered beta regression model converged and provided an acceptable fit to the data, as evidenced by the posterior density checks (Figures 4 & 5). Estimates for vigilance varied from 0.208-0.239 in the non-hunted populations and 0.204-0.322 in the hunted populations. Point estimates are provided as posterior medians (Table 4). The mean proportion of animals vigilant for the populations described by the 5 hunting profiles were roughly comparable to each other and ranged from 0.235 for hunting profile # 1 to 0.273 for hunting profile # 4 (Table 5). The ROPE + HDI Decision Rule with a pre-defined ROPE Range of (-0.20, +0.20) and the favored 89% HDI revealed that equivalence – or, alternatively, negligibility of effects – was accepted for all comparisons of interest (Figure 6). Using the 95% HDI in conjunction with the same rule revealed equivalence for all comparisons except for Comparisons 3 and 6.

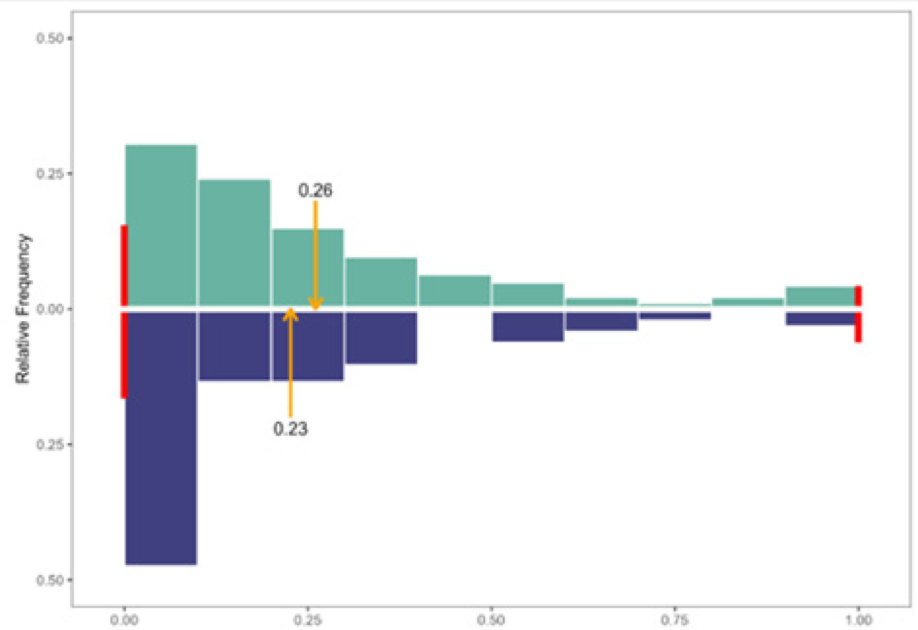

Figure 1: Distribution of mean value of vigilance (Average Proportion Heads Up) of adult bison during the period of observation, compared across hunted (top panel) and non-hunted (bottom panel) locations in South Dakota, North Dakota, and Montana from 2018-2021. Weighted mean values of vigilance are indicated via vertical lines.

The ROPE + HDI decision rule with a varying rather than pre-defined Rope Range and both 89% and 95% HDI produced the following results (Table 3 & Figure 7). For Comparison 1, -the minimal ROPE Radius beyond which the effect of Hunting Status (Hunting vs No Hunting) on bison vigilance could be considered negligible - was at least 0.140 (89% HDI) and 0.161 (95% HDI). Comparisons 2, 3 and 4 - determined the minimal ROPE Radius beyond which the effect of Recent Hunting History (# months since last hunt) on bison vigilance could be considered negligible. Comparison 2 indicates that the effect of a Recent Hunting History of 4.5 Months Prior to Current Month, relative to current month, is negligible for a ROPE radius of at least 0.116 (89% HDI) and

0.152 (95% HDI). Comparison 3 implies that the effect of a Recent Hunting History of 7+ Months Prior to Current Month, relative to current month, can be considered negligible for a ROPE radius of at least 0.171 (89% HDI) and 0.215 (95% HDI). Comparison 4 shows that the effect of a Recent Hunting History of 7+ Months Prior to Current Month, relative to 4.5 Months Prior to Current Month, can be considered negligible for a ROPE radius of at least 0.137 (89% HDI) and 0.174(95% HDI) (Table 6). Finally, Comparisons 5, 6 and 7 (Figure 2 & Table 3) enabled determination of the minimal ROPE Radius beyond which the effect of Number of Hunt Months on bison vigilance could be considered negligible. Comparison 5 revealed that the effect of 6 or fewer hunt months relative to 0 hunt Months is negligible for a ROPE radius of at least 0.148 (89% HDI) and 0.164 (95% HDI). Comparison 6 indicated that the effect of 12 Hunt Months relative to 0 Hunt Months is negligible for a ROPE radius of at least 0.175 (89% HDI) and 0.246 (95% HDI). Comparison 7 revealed that the effect of 12 Hunt Months relative to ≤ 6 Months is negligible for a ROPE radius of at least 0.151 (89% HDI) and 0.203 (95% HDI).

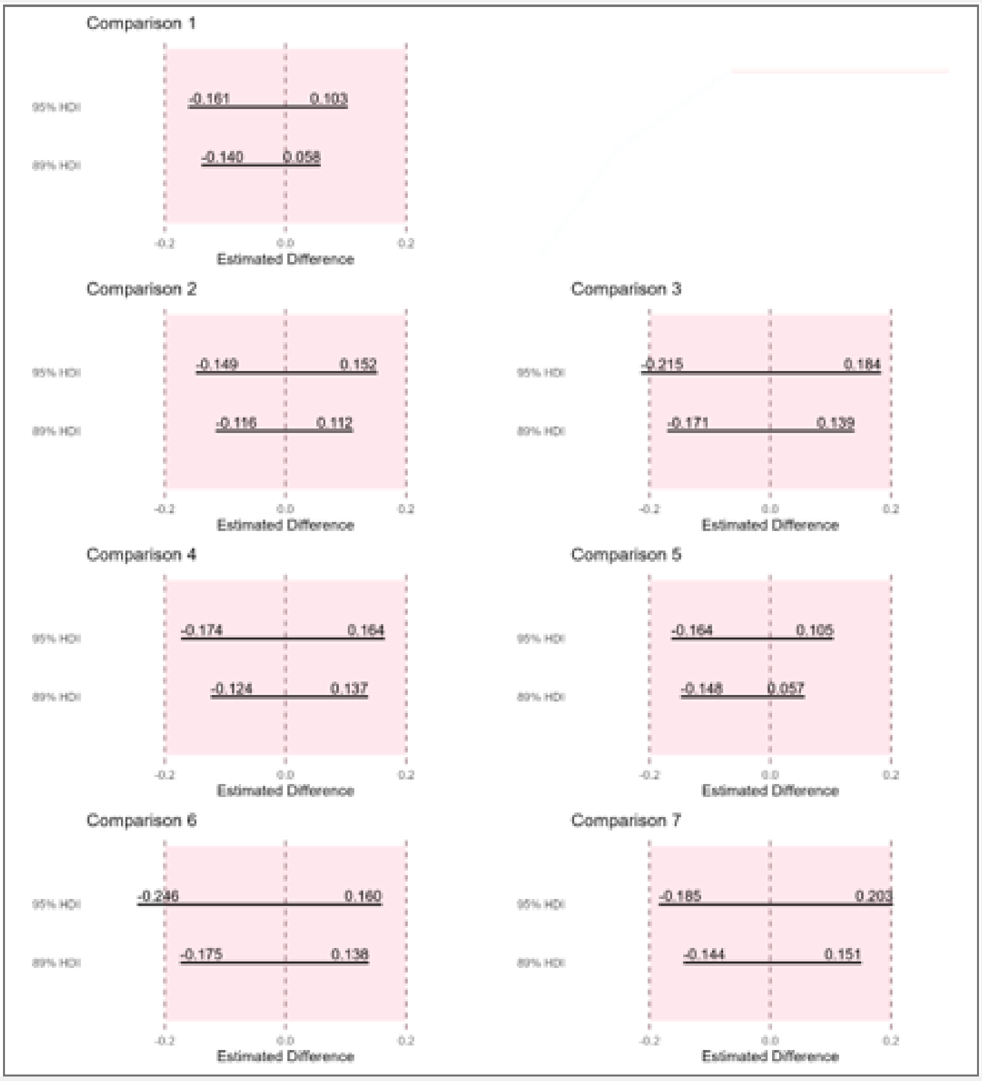

Figure 2: Plots displaying the 89% HDI and the 95% HDI as segments with annotated endpoints for each comparison of interest in relation to the pre-specified ROPE Range of -0.20 to 0.20.

Discussion

We investigated vigilance of bison in non-hunted and hunted populations as well as among hunted populations that were subjected to different hunting pressure. Nearly all of the comparisons indicate that vigilance of bison was essentially equal among populations regardless of hunting pressure (Table 3 & Figure 2). Sarno [28] originally reported a negative relationship between year-round human hunting and bellowing rate (i.e., vocal advertisement) of bison bulls during the reproductive season. Since one aspect of male bison reproductive behavior was negatively associated with hunting, is it surprising that bison vigilance is not? Various ungulates, including Roe deer (Capreolus capreolus), Red deer (Cervus elaphus), Mediterranean mouflon (Ovis gmelini musimon x Ovis sp.), Fallow Deer (Dama dama), Blue Sheep (Bharal) (Pseudois nayaur) and Impala (Aepyceros melampus) adjust their vigilance in relation to hunting by humans Benhaiem [5], Jayakody [17], Benoist [16], Stankowich [12]. Furthermore, vigilance time of impalas was also longer on a property where they were hunted by humans more frequently than on an adjacent property with reduced hunting Stankowich [12]. Given these data, one might predict that bison vigilance will also increase in areas where there is human hunting. Because bison exhibit strong constitutive defenses (i.e., large and hard to kill), however, we originally predicted that vigilance would not vary among bison populations regardless of hunting status. Constitutive defenses, like large body size, are always "on". As a result, adult bison may not substantially alter their vigilance even when faced with predators because their large size provides some protection against predation, while also providing a good vantage point from which to survey their surroundings.

Table 4: Estimated values (i.e., posterior medians), 89% and 95% highest density intervals (HDI) for the mean value of vigilance (i.e., Average Proportion Heads Up) at each of the 12 bison study locations.

Location	Estimate	89% HDI	95% HDI
BNP	0.239	(0.226, 0.252)	(0.224, 0.255)
CSP	0.278	(0.255, 0.301)	(0.248, 0.305)
FLY-D	0.262	(0.250, 0.276)	(0.246, 0.278)
LBR-BGU	0.277	(0.234, 0.321)	(0.228, 0.335)
LBR-CRU	0.321	(0.277, 0.364)	(0.273, 0.381)
LBR-HRU	0.299	(0.261, 0.340)	(0.252, 0.350)
PR-YB	0.204	(0.186, 0.221)	(0.183, 0.226)
SGU-S	0.468	(0.435, 0.499)	(0.429, 0.507)
SRR-N	0.215	(0.193, 0.237)	(0.188, 0.243)
SRR-W	0.322	(0.273, 0.373)	(0.261, 0.384)
TRNP	0.209	(0.181, 0.238)	(0.174, 0.243)
WICA	0.208	(0.189, 0.225)	(0.185, 0.230)

Table 5: Estimated values (i.e., posterior medians) and 89% and 95% highest density intervals (HDI) for the mean value of group-level vigilance (Average Proportion Heads Up), for 12 bison populations described by the 5 hunting profiles.

Hunting Profile	Estimate	89% HDI	95% HDI
1	0.235	(0.163, 0.316)	(0.140, 0.342)
2	0.274	(0.198, 0.352)	(0.181, 0.378)
3	0.271	(0.183, 0.380)	(0.148, 0.402)
4	0.257	(0.131, 0.399)	(0.097, 0.449)
5	0.273	(0.150, 0.395)	(0.124, 0.440)

Berger and Cunningham [29] reported that, in an area with four sympatric native North American ungulates including bison, pronghorn antelope, (Antilocapra americana), Bighorn sheep (Ovis canadensis), and mule deer (Odocoileus hemionus), smaller-bodied ungulates were more vigilant than larger-bodies ones. Furthermore, vigilance of bison in areas with and without wolves did not differ. This lends credence to our hypothesis that bison vigilance will not vary between hunted and non-hunted locations due to bison possessing strong constitutive defenses. The invocation of constitutive defenses may not entirely explain the lack of increased vigilance, however. Vigilance is also costly due to concomitant reductions in foraging time Jennings & Evans [48]; Underwood [49]; Berger and Cunningham [29]; Lima [6]; Abramsky [50], Fortin [51]. While all species need to balance antipredator behavior and foraging efforts across varying levels of risk Lima and Bednekoff [52], large-bodied ones, like bison - needing to satisfy large daily dietary requirements - may be particularly limited with respect to how much they can increase vigilance. However, while vigilance is costly for bison, because feeding rate diminishes with increasing vigilance, it does not

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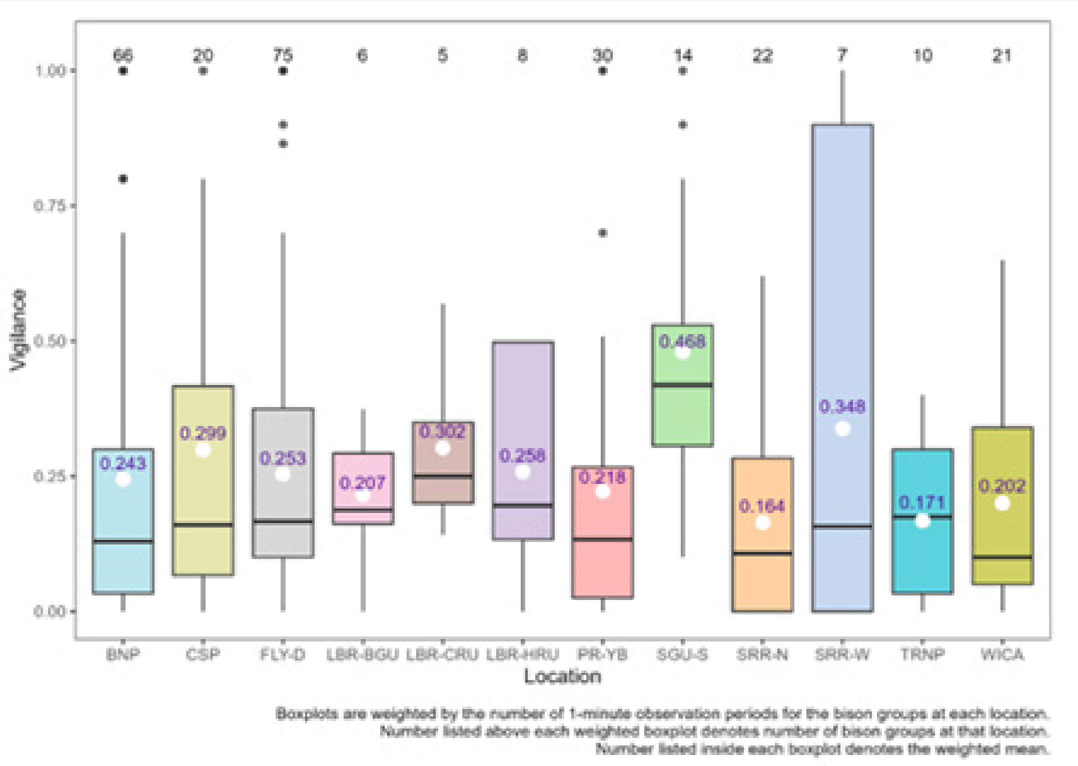
appear to be as costly as previously assumed Fortin [51]. It is often assumed that human hunters exert the same influence (functional redundancy) on their prey as do native carnivores Berger [1], Clinchy [2]; various reports demonstrate that ungulates can show stronger behavioral responses to human predators than to predation risk posed by large carnivores Proffitt [3], Ciuti [4] Yet, our data indicate that bison vigilance (at least how we measured it) was not influenced by human hunting. While sample size is low, data from 2 bison populations with wolves or wolves and grizzly bears indicate that vigilance is essentially equal between these populations and those without predators and with/without human hunting. In other words, predation by humans and native carnivoress appears to be functionally redundant in the populations that we have observed.



Boxplots are weighted by the number of 1-minute observation periods for the bison groups at each location.
Number listed above each weighted boxplot denotes number of bison groups at that location.
Number listed inside each boxplot denotes the weighted mean.

Figure 3: Distribution of vigilance (i.e., Average Proportion Heads Up) of adult bison during the period of observation by location in South Dakota, North Dakota, and Montana from 2018-2021.

Table 6: Estimated values (i.e., posterior medians) along with 89% and 95% highest density intervals (HDI) for the effects quantified by comparisons 1 through 7 involving the mean value of the response variable in bison populations having hunting profiles 1 through 5.

Comparison	Comparison Details	Estimate	89% HDI	95% HDI
Effect of Hunting Status:				
1	No vs Yes	-0.035	(-0.140, 0.058)	(-0.161, 0.103) NO?
Effect of Number of Recent Hunting History:				
2	Current Month vs 4.5 Months Prior	-0.008	(-0.116, 0.112)	(-0.149, 0.152) NO
3	Current Month vs 7+ Months Prior	-0.008	(-0.171, 0.139)	(-0.215, 0.184)
4	4.5 Months Prior vs 7+ Months Prior	0	(-0.124, 0.137)	(-0.174, 0.164)
Effect of Number of Hunt Months:				
5	0 Months vs 6 Months	-0.037	(-0.148, 0.057)	(-0.164, 0.105)
6	0 Months vs 12 Months	-0.022	(-0.175, 0.138)	(-0.246, 0.160)
7	6 Months vs 12 Months	0.018	(-0.144, 0.151)	(-0.185, 0.203)

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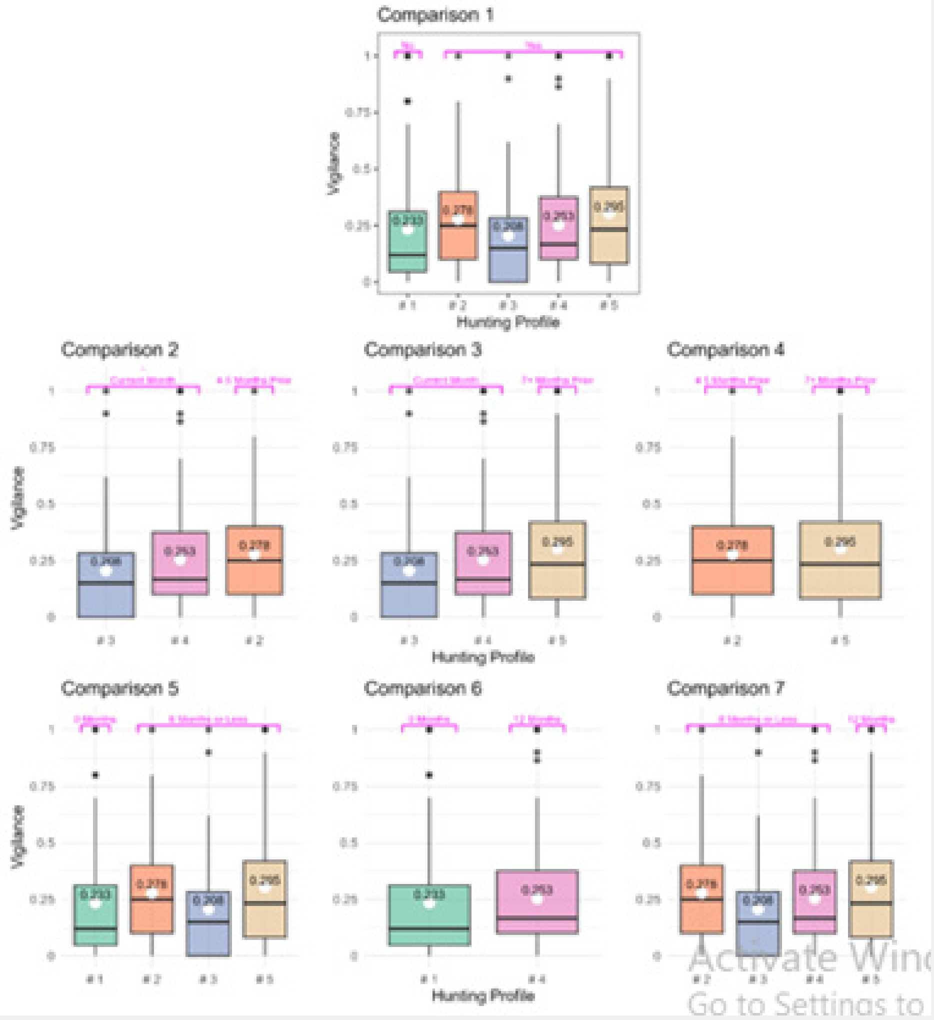

Figure 4: Data-driven comparisons of interest performed between sets of bison populations in our study sharing the same hunting profile.

Also, group size appeared to have no effect on vigilance. For many species of birds and mammals vigilance tends to decrease as a function of group size Elgar [53]; Quenette [13], Beauchamp [54]. However, the assumed relationship between these two variables is not so straightforward. For example, vigilance is also influenced by body size, with smaller bodied animals being more vigilant than larger bodied ones Berger and Cunningham [29], Luo [55]. In addition to surveilling for predators, vigilance appears to serve various functions, which include searching for mates Burger and Gochfeld [56] potential competitors Valone and Wheel Barger [57], offspring defense Burger and Gochfeld [56], and evaluating habitat quality Smith [58] among others. Perhaps it is possible that background predation risk in our study was insufficient to induce increased vigilance in bison. Despite our assertion that bison vigilance does not appear associated with human hunting, it would be naïve to think that human hunting of bison is without its impacts. On multiple occasions (in populations subjected to year-round hunting) we observed all bison moving together throughout the day. Because hunts were conducted using motor vehicles (pickup trucks and ATV's), bison had only temporary refuge during hunting events, even in heterogeneous landscapes. Furthermore, reduced reproductive output Pauli and Buskirk [24], French [25] resulting from chronic predation risk Schmidt and Kuijper [59] and elevated stress may be occurring; calving rate of bison in year-round hunted populations varied between 20-56%. Calving rate in populations that are hunted < 6 months/year was 70-90%. While other variables like nutrient deficiencies Corah and Ives [60] may negatively impact bison reproduction, the disparity in calving rates between bison populations that are hunted year-round and those hunted < 6 months/year is cause for more scrutiny. We are in the midst of assessing fecal-glucocorticoid levels in an attempt to investigate stress in populations subjected to different hunting pressures.

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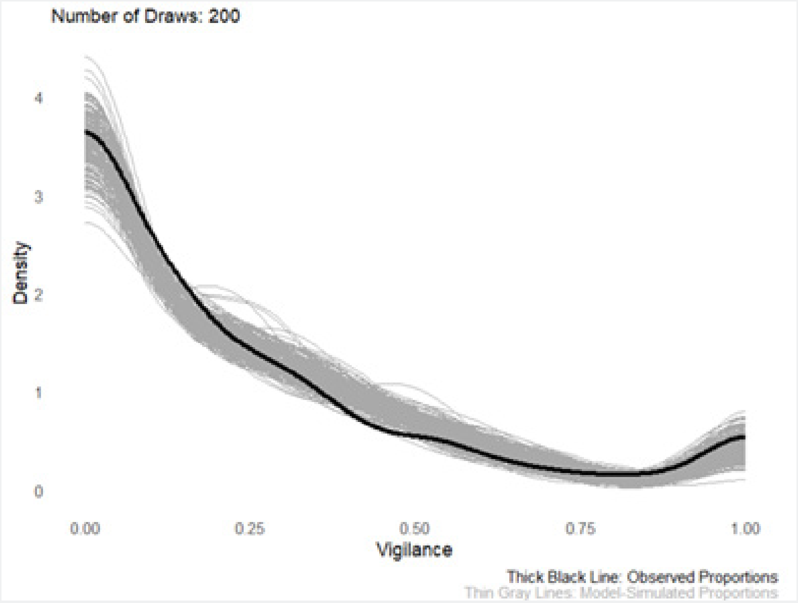

Figure 5: Posterior predictive check for all 12 study locations combined.

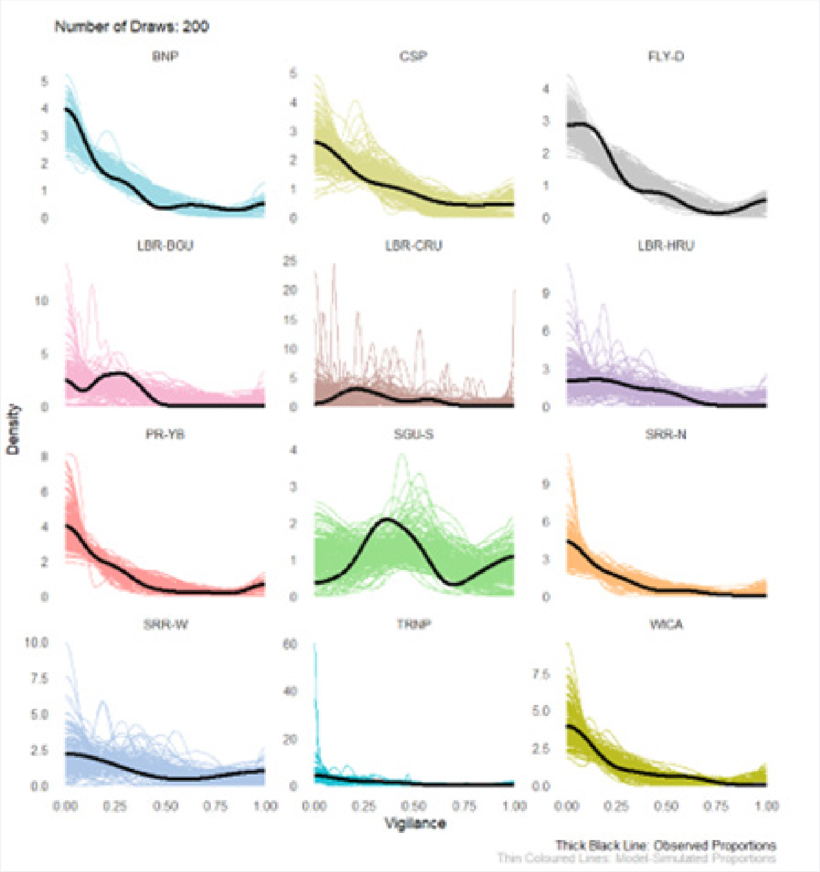

Figure 6: Posterior predictive check for each of the 12 study locations.

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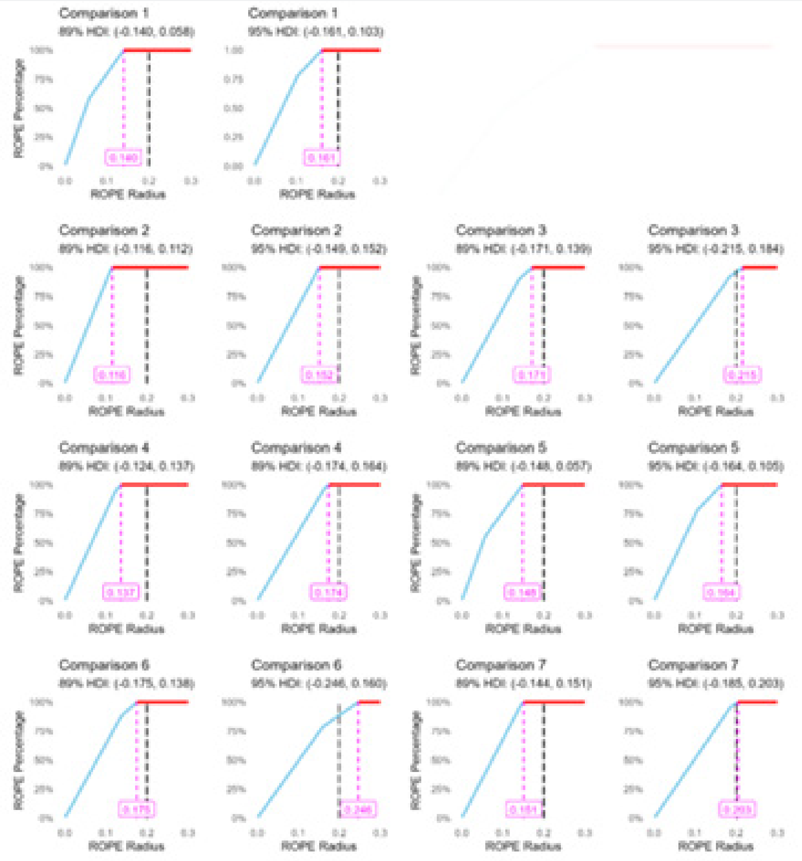

Figure 7: Plots of ROPE Percentage versus ROPE Radius for each comparison of interest for the 89% HDI and the 95% HDI, with a ROPE Radius of 0.20 (vertical black line) indicated alongside the minimum ROPE Radius (vertical magenta line and corresponding number) beyond which the null hypothesis of equivalence would be accepted.

Human exploitation (i.e., hunting and fishing) has induced striking changes in phenotype and life-history traits in only decades Darimont [61]. Yet, there is relatively little known about how hunting influences the behavior of survivors in the numerous species of ungulates that are hunted globally Cromsigt [62]; Ripple [63], especially populations that are confined to game ranches and state parks. Many of these 'captive' populations can offer unique opportunities to study prey responses to human predation risk Lima and Dill [5], Lima and Bednekoff [48], Creel [64]. For example, the variability among researchers in the characterization of risk influences interpretation, thus limiting the ability to make comparisons among studies Moll [65], Prugh [66], Ferrari [67]. Furthermore, difficulties quantifying core parameters such as predator encounter rate, probability of death given an encounter, and temporal variability of risk can be more easily estimated (or may be already known) , especially if humans are the only important source of predation. While the most proximate impacts of human-hunting are changes in population size and demography, insidious behavioral changes may yield consequences from which hunted populations cannot easily recover. Although data are accumulating, it is still too early to determine to what extent subtle shifts in behavior as a result of human hunting could induce a cascade of unforeseen outcomes at the population, community, and ecosystem level Hawlena and Schmitz [68], Wilson [69], Tablado and Jenni [70].

Acknowledgments

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