

Factors affecting gray wolf (*Canis lupus*) encounter rate with elk (*Cervus elaphus*) in Yellowstone National Park

H.W. Martin, L.D. Mech, J. Fieberg, M.C. Metz, D.R. MacNulty, D.R. Stahler, and D.W. Smith

Abstract: Despite encounter rates being a key component of kill rate, few studies of large carnivore predation have quantified encounter rates with prey, the factors that influence them, and the relationship between encounter rate and kill rate. The study's primary motivation was to determine the relationship between prey density and encounter rate in understanding the mechanism behind the functional response. Elk (*Cervus elaphus* Linnaeus, 1758) population decline and variable weather in northern Yellowstone National Park provided an opportunity to examine how these factors influenced wolf (*Canis lupus* Linnaeus, 1758) encounter rates with elk. We explored how factors associated with wolf kill rate and encounter rate in other systems (season, elk density, elk group density, average elk group size, snow depth, wolf pack size, and territory size) influenced wolf–elk encounter rate in Yellowstone National Park. Elk density was the only factor significantly correlated with wolf–elk encounter rate, and we found a nonlinear density-dependent relationship that may be a mechanism for a functional response in this system. Encounter rate was correlated with number of elk killed during early winter but not late winter. Weak effects of snow depth and elk group size on encounter rate suggest that these factors influence kill rate via hunting success because kill rate is the product of hunting success and encounter rate.

Key words: wolf, *Canis lupus*, elk, *Cervus elaphus*, encounter rate, Yellowstone, functional response.

Résumé : Si la fréquence des rencontres est un élément clé du taux de prédation, peu d'études sur la prédation par de grands carnivores ont quantifié la fréquence des rencontres avec des proies, les facteurs qui l'influencent et la relation entre la fréquence des rencontres et le taux de prédation. La principale motivation de l'étude consistait à établir la relation entre la densité de proies et la fréquence des rencontres pour mieux comprendre le mécanisme qui sous-tend la réaction fonctionnelle. Le déclin de la population de wapitis (*Cervus elaphus* Linnaeus, 1758) et la météo variable dans le secteur nord du Parc national de Yellowstone offrent la possibilité d'examiner l'influence de ces facteurs sur la fréquence des rencontres de loups (*Canis lupus* Linnaeus, 1758) avec des wapitis. Nous avons examiné l'influence de facteurs associés au taux de prédation par des loups et à la fréquence des rencontres dans d'autres systèmes (saison, densité des wapitis, densité des groupes de wapitis, taille moyenne des groupes de wapitis, épaisseur de la neige, taille de la meute de loups et dimension du territoire) sur la fréquence des rencontres loup-wapiti dans le Parc national de Yellowstone. La densité des wapitis est le seul facteur qui présente une corrélation significative avec la fréquence des rencontres loup-wapiti, et nous avons noté une relation non linéaire dépendante de la densité qui pourrait constituer un mécanisme de réaction fonctionnelle dans ce système. La fréquence des rencontres est corrélée au nombre de wapitis tués au début de l'hiver mais non à la fin de l'hiver. De faibles effets de l'épaisseur de la neige et de la taille des groupes de wapitis sur la fréquence des rencontres semblent indiquer que ces facteurs influencent le taux de prédation par l'entremise du succès de la chasse étant donné que le taux de prédation est le produit du succès de la chasse et de la fréquence des rencontres. [Traduit par la Rédaction]

Mots-clés : loup, *Canis lupus*, wapiti, *Cervus elaphus*, fréquence des rencontres, Yellowstone, réaction fonctionnelle.

Introduction

Quantifying predator–prey interactions is essential to determining the effect of predation on prey populations. For interactions involving large carnivores, the relationship between prey density and the number of prey killed per predator per unit time (kill rate) is of particular importance. This relationship, known as the functional response, can be broken down into search rate and handling time (Holling 1959). A central assumption of the models describing the functional response is that the number of prey

encountered is related to prey density; however, this assumption has been largely untested (Lotka 1925; Nicholson 1933; Pyke et al. 1977; Stephens and Krebs 1986).

Holling (1959) defined three types of functional responses: Type I is one in which the number of prey killed per predator is directly proportional to prey density until abruptly reaching a maximum rate, in Type II, the number of prey killed per predator increases rapidly with prey density and then increases more slowly until it reaches a threshold (limited by the time it takes to process prey).

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and Type III is one in which the number of prey killed per predator first increases with prey density and then decreases (a sigmoidal curve). Most studies of wolf-prey systems report a Type II response, which assumes that encounter rate limits kill rate at low prey densities, but at high prey densities, kill rate is limited by the handling time required for wolves to consume and digest their prey, leading to a relatively constant kill rate (Holling 1959; Dale et al. 1994; Messier 1994; Hayes et al. 2000; Messier and Joly 2000). However, wolf (*Canis lupus* Linnaeus, 1758) kill rates are also affected by pack size (Thurber and Peterson 1993), winter severity (Mech et al. 2001), and season (Smith et al. 2004; Metz et al. 2012), making the relationship between prey density and kill rate difficult to disentangle (Mech et al. 2001; Smith et al. 2004; Vucetich et al. 2011; Metz et al. 2012).

While the relationship between kill rate and prey density is highly variable, with many other factors influencing kill rate (Mech et al. 2001; Smith et al. 2004; Metz et al. 2012), we expect that encounter rate and kill rate vary with prey density (Holling 1959; Dale et al. 1994; Messier 1994; Hayes et al. 2000; Messier and Joly 2000). The lack of studies observing encounter rates in large carnivore systems warrants further examination of this mechanism linking prey density to kill rate (Holling 1959).

Here we quantify predator-prey interactions and assess factors affecting wolf-elk encounter rates in the Northern Range (NR) of Yellowstone National Park (YNP) to determine if encounter rate is an important mechanism linking prey density and kill rate. We assess the effect that prey density, wolf pack size, and winter severity (factors known to affect wolf kill rates) as well as wolf pack territory size, and elk (*Cervus elaphus* Linnaeus, 1758) group size (factors known to affect encounter rate) have on encounter rates.

While quantifying encounter rate and understanding the factors affecting it are important to understanding predator-prey interactions, predatory behavior, and predation risk, the ability to quantify encounter rates in other systems will be difficult. We take advantage of a long-term (9 year) data set in YNP to determine if encounter rate is correlated with kill rate and how this relationship may be linked to the underlying functional response in Yellowstone's wolf-prey system. Additionally, quantifying the relative importance of these different factors might help with understanding how predation rate will change under changing environmental conditions.

Objectives

Our objectives are (1) to determine how wolf pack encounter rates of elk are affected by season, elk density, elk group density, average elk group size, snow depth, wolf pack size, and territory size and (2) to understand how encounter rates affect wolf kill rate and to what extent encounter rate may be a mechanism that drives the wolf functional response.

After reviewing the literature and comparing the NR of YNP with other systems, we developed several a priori models with which to assess the effects of season, elk density, elk group density, average elk group size, snow depth, wolf pack size, and territory size on encounter rate. We expected that encounter rates would be higher when the snow pack is more severe, which limits elk movement and distribution (Sweeney and Sweeney 1984; Coughenour and Singer 1996; Eriksen et al. 2009) and in late winter when elk are in poor nutritional condition (DelGiudice et al. 1991; Cook et al. 2004). We hypothesized that elk density, elk group density, and average group size would have a positive effect on encounter rates because it is easier for wolves to locate larger groups of elk that congregate in predictable locations (Huggard 1993; Hebblewhite and Pletscher 2002) but that the relationship between elk density and encounter rate may be nonlinear due to the amount of time required to search for and attack elk (Holling 1959). We hypothesized that an increase in wolf pack size would lead to a larger search radius (Hassell and Varley 1969; Cosner et al. 1999) and increased motivation to encounter prey due to

biomass acquisition per individual being lower in larger packs (Thurber and Peterson 1993; Kuzyk et al. 2005), and therefore, large packs would have higher encounter rates. We also expected that wolves with larger winter territories would have lower encounter rates due to more dispersed prey and the necessity to cover more ground in search of prey. While territory size is often correlated with prey density (Schmidt et al. 2007; Kittle et al. 2015), intrapack conflict is common in the study area and influences territory size and wolf population dynamics (Cubaynes et al. 2014; Cassidy et al. 2015). Overall, we expected that encounter rate would have a positive effect on kill rate.

Study area

The NR herd is the largest in the park, and its wintering range, the NR, extends west from the Lamar Valley to 6 Mile Creek, northeast of Dome Mountain (total area = 1526 km²) (Houston 1982; Lemke et al. 1998; Cook et al. 2004). From 1995 to 2013, the winter count inside the park declined from 17 740 to 1585 elk (Tallian et al. 2017). The study area includes the portion of the NR inside YNP, Wyoming (Fig. 1). Elevations range from 1500 to 2400 m with the lower and upper elevations characterized by wide river valleys and open slopes, mountain tops, valleys, and plateaus, respectively. Plant communities consist of coniferous forests at higher elevations (lodgepole pine (*Pinus contorta* Douglas ex Loudon), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and whitebark pine (*Pinus albicaulis* Engelm.)) and grasslands and big sagebrush (*Artemisia tridentata* ssp. *Vaseyana* (Rydb.) Beetle) at lower elevations (Despain 1990). Winters are long and cold, and total snowfall is less than 500 cm, varying with elevation and location (Farnes and Shafer 1975).

The NR is inhabited by a diverse suite of ungulates, including elk, moose (*Alces americanus* (Clinton, 1822)), bison (*Bison bison* (Linnaeus, 1758)), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), and pronghorn (*Antilocapra americana* (Ord, 1815)) preyed upon by wolves, grizzly bears (*Ursus arctos* Linnaeus, 1758), cougars (*Puma concolor* (Linnaeus, 1771)), coyotes (*Canis latrans* Say, 1823), and black bears (*Ursus americanus* Pallas, 1780). Wolves' primary prey is elk, comprising over 89% of kills in spring, 85% in summer, and 96% during winter (Metz et al. 2012).

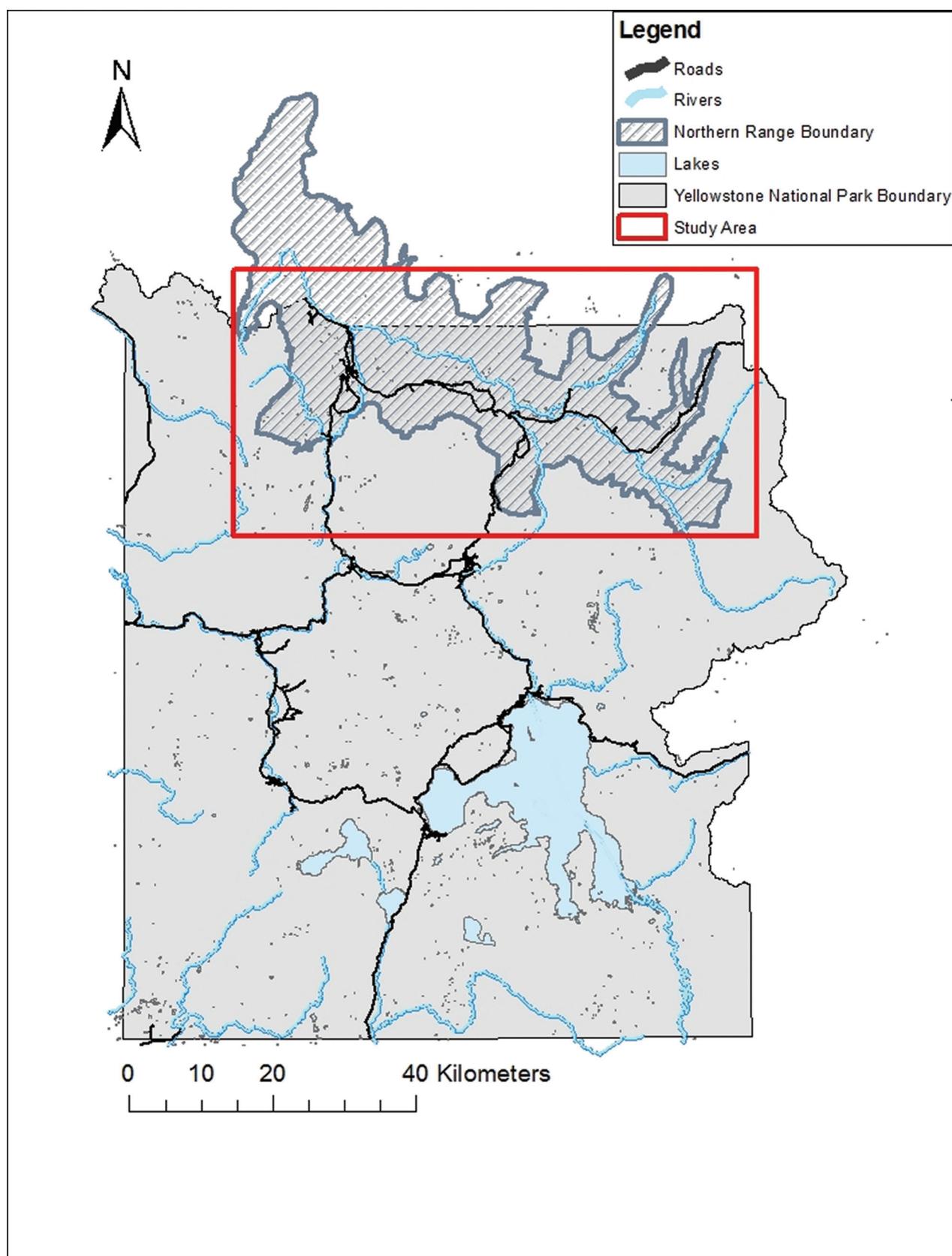
Materials and methods

Data collection

Yellowstone maintains very high frequency and global positioning system radio collars on approximately 20% of its wolf population. These wolves were aerially darted following the capture and handling protocols recommended by the American Society of Mammalogists (Sikes et al. 2016) and approved by a National Parks Service animal handling committee. Since 1996, Yellowstone air and ground crews annually monitored movements of two or three wolf packs daily on the NR from 15 November to 14 December and from 1 to 30 March via aerial and ground radio telemetry. Ground crews monitored packs from sunrise to sundown to collect data on wolf travel behavior, wolf-prey interaction, and kill rate (see Smith and Bangs 2009). The two or three wolf packs observed each winter involved 11 different packs over the nine winters of the study. This resulted in 46 pack study periods (i.e., pack A observed during early winter in one year equals one pack study period) over nine winters (2004–2012).

Crews of trained biologists observed wolf-prey interactions from 200 to 6000 m via spotting scopes and voice recorded data that were later transcribed onto forms. From these accounts of behavior and interactions, we used the total number of wolf-elk encounters for each pack along with daily wolf activity summaries and maps of wolf movement. The majority of wolf hunting

Fig. 1. Yellowstone National Park, the wintering area of the Northern Yellowstone elk (*Cervus elaphus*) herd or Northern Range, and the study area.



activity occurs during the morning (dawn) and evening hours (dusk) during which crews made observations (Kohl et al. 2017).

We estimated pack kill rate (number of prey killed per pack per day) via an index method that characterized the number of elk kills per pack per index day, which represented the number of days that the wolves were visually located by the ground crew or radio or visually located by the aerial crew. Using these index values of elk kills per pack per day, we estimated the total number of elk kills expected during the study to account for differences in the number of successful observation days between packs.

We defined a wolf–elk encounter as the observation of a wolf pack interacting with elk in any of the following foraging states (MacNulty et al. 2007): (1) approach (fixating on and traveling toward prey), (2) watch (fixating on prey while not traveling), or (3) attack (running after a fleeing group or individual or lunging at a standing group or individual).

Crews of trained biologists recorded daily activity summaries or time budgets of observed behaviors exhibited by each wolf pack, including time spent traveling, resting/sleeping, hunting, feeding, howling, and other, and a pack was assigned a particular behavior based on how the majority of the pack was behaving. Field crews recorded the locations of daily activities on US Geological Survey 7.5 min, quadrangle topographic maps and drew travel routes, creating daily activity maps that matched the daily activity summaries. We cleaned the daily activity summary database using a protocol to detect any errors. We digitized the daily activity maps for study packs using ArcGIS. We derived the time that wolves were observed traveling from these maps by linking the daily activity summaries and daily activity maps using linear referencing in ArcGIS (Scarponeini 2002). The total time that wolves were observed traveling was considered searching behavior, and we excluded all travel associated with kill sites (MacNulty et al. 2007). In digitizing, we cross-referenced the wolf kill data set, daily activity summaries, and daily activity maps to identify kill locations, record wolf group size, and determine if the wolves were at a kill during recorded activities.

We created an index of winter territory size for the wolf packs observed using aerial and ground telemetry locations from 1 November to 31 March. If wolf packs were split, locations of both groups were kept in the analysis to account for the total area occupied by the pack. We used the package “adehabitat” in R to create 90% isopleths of kernel density estimates using the ad hoc method to estimate smoothing parameters for territory size (Börger et al. 2006; Calenge 2006), considering the associated areas as a relative index of space use (Fieberg and Börger 2012; Signer et al. 2015).

The Northern Yellowstone Cooperative Wildlife Working Group conducted annual winter (16 December – 26 February) elk counts in the study area (White et al. 2011). We calculated mean, median, and 70th quantiles of group size, elk group density, and elk density in each wolf pack’s territory by intersecting 90% isopleths of kernel density with the locations of elk groups seen in the corresponding winter year. Winter elk migration occurs before the annual count, so a single count provides an index of mean group size and relative elk abundance in each pack’s territory (White et al. 2010).

We used average snow water equivalent (SWE) as an index of snow depth and winter severity (snowpack severity), which we calculated for each wolf pack territory using modeled SWE from the National Weather Service’s Snow Data Assimilation System with 1 km spatial resolution and 24 h temporal resolution from the winter years of 2004–2012 (National Operational Hydrologic Remote Sensing Center 2004). We calculated snowpack severity for each season and wolf pack territory by taking the daily mean SWE within a wolf pack territory.

Data analysis

We used Bayesian generalized linear mixed effects models to explore relationships between encounter rates and SWE, elk density, elk group density, elk group size, wolf pack territory size, and pack size. We assumed, conditional on the random effects, that the number of elk encounters that a wolf pack had during a study period followed a negative binomial distribution to allow for overdispersion. This allowed for the fact that the elk encounter data were overdispersed relative to a Poisson distribution. We included random effects for pack and winter year. We centered and scaled all of the variables so we could directly compare the effect size of variables (Schielzeth 2010) and to improve mixing of the Monte Carlo Markov chains (Kery 2010). We initially explored including the log of time observed traveling as a fixed effect to account for the amount of time that wolves were observed searching for elk. The estimated regression coefficient was close to 1 (0.95, 95% credible interval = 0.64, 1.30). Because the credible interval included 1, we chose to model log of time observed traveling as an offset, effectively modeling encounter rates for individual pack study periods as the response variable (McCullagh and Nelder 1989).

We evaluated a series of generalized linear mixed effects models relating log of elk encounter rates to variables that capture (1) elk abundance and distribution (elk density, elk group density, average elk group size, and SWE) (Sweeney and Sweeney 1984; Boyce 1991; Huggard 1993; Cosner et al. 1999; Schaefer 2000; Hebblewhite and Pletscher 2002; Fryxell et al. 2007) and (2) wolf pack space use (winter territory size) and prey detectability (pack size, which influences detection radius; see above) (Hassell and Varley 1969; Cosner et al. 1999; Hayes et al. 2000; Kuzyk et al. 2005). Due to correlation between measures of elk abundance (elk density, elk group density, and average elk group size), we evaluated one model that included elk density to describe elk abundance and another using elk group density and average elk group size. The elk density model (elk density + season + territory size + SWE + wolf pack size) used the elk density within a pack’s territory. The elk group density and size model used elk group density and the average elk group size within a pack’s territory (elk group density + average elk group size + wolf pack territory size + season + SWE + wolf pack size). We also tested for a relationship between hourly encounter rate and the estimated number of elk killed by a wolf pack during the study period using linear regression.

We examined the posterior distributions of the random year effects to explore year-to-year variability in encounter rates not explained by the fixed effects. These year effects measure annual deviations from the overall mean log encounter rate.

We tested for a nonlinear relationship between elk (and group) density and encounter rates by adding a quadratic term for elk (and group) density. In addition, we considered alternative measures of elk group size as a sensitivity analysis to determine the importance of group size to encounter rates using the median and 70th percentile instead of mean group size to account for the often right-skewed distribution of ungulate group sizes (Brennan et al. 2015). As a post hoc analysis, we modeled the effect of elk density on log encounter rates by fitting a linear spline with an asymptotic slope of 0 using an uninformative prior distribution for the breakpoint estimate within the model to determine the elk density that maximized encounter rates.

We used data from 46 pack study periods over nine winters (2004–2012), 24 from early winter and 22 from late winter (Table 1). On average, 2.56 packs (range 1–3) were observed for two 30 day periods each year for an average of 108.40 h (SD = 43.45) within each of the two 30 day periods and were observed traveling for 13.47 h per study period (range 2.85–27.82, SD = 6.20). We used estimates of elk density (mean = 3.88 elk/km², SD = 2.75), group density (mean = 0.21 groups/km², SD = 0.11), average elk group size (mean = 16.52, SD = 5.83), and SWE (mean = 11.89 cm, SD = 9.28) to characterize elk distribution within a pack territory. We used

Table 1. Wolf (*Canis lupus*) pack encounters and kills of elk (*Cervus elaphus*) and the biotic and abiotic factors hypothesized to affect them on the Northern Range of Yellowstone National Park, winter years 2004–2012.

Pack name	Study ^a	Winter year	Elk encounters	TIV travel ^b	Territory size (km ²) ^c	Average elk group size	Median elk group size	70th percentile of elk group size	Mean SWE (cm) ^d	Elk group density	Encounters per minute	Elk density	Estimated elk kills ^e	Pack size	Index of elk kills per day ^f
Druid Peak	March	2004	17	820	291.13	31.48	10.50	17.00	151.12	0.21	0.02	6.49	11.1	13	0.37
Geode Creek	March	2004	6	446	186.02	24.73	16.00	29.20	133.16	0.32	0.01	7.84	11.4	6	0.38
Leopold	March	2004	19	933	196.21	22.15	8.00	22.20	122.07	0.49	0.02	10.95	11.7	17	0.39
Druid Peak	November–December	2004	36	1669	291.13	31.48	10.50	17.00	44.00	0.21	0.02	6.49	19.2	17	0.64
Geode Creek	November–December	2004	3	353	186.02	24.73	16.00	29.20	36.57	0.32	0.01	7.84	11.7	8	0.39
Leopold	November–December	2004	10	753	196.21	22.15	8.00	22.20	29.15	0.49	0.01	10.95	13.2	19	0.44
Geode Creek	March	2005	11	692	249.51	15.58	10.00	16.00	114.46	0.25	0.02	3.87	14.4	11	0.48
Leopold	March	2005	24	1179	264.50	20.40	10.00	17.00	116.35	0.35	0.02	7.10	10.8	25	0.36
Slough Creek	March	2005	22	1370	253.21	17.02	10.00	16.60	111.81	0.23	0.02	3.97	12.3	15	0.41
Druid Peak	November–December	2005	16	1427	452.86	17.87	10.00	17.70	40.54	0.14	0.01	2.45	6.6	11	0.22
Geode Creek	November–December	2005	3	299	249.51	15.58	10.00	16.00	36.20	0.25	0.01	3.87	11.7	13	0.39
Leopold	November–December	2005	14	836	264.50	20.40	10.00	17.00	34.50	0.35	0.02	7.10	12	24	0.40
Hellroaring	March	2006	13	793	328.12	20.05	10.00	18.50	197.01	0.20	0.02	4.03	9.6	7	0.32
Leopold	March	2006	17	990	126.71	15.52	9.00	17.40	160.17	0.26	0.02	4.04	13.5	7	0.45
Slough Creek	March	2006	24	1312	346.28	12.06	7.00	13.40	209.84	0.10	0.02	1.22	9.6	12	0.32
Leopold	November–December	2006	22	923	126.71	15.52	9.00	17.40	56.53	0.26	0.02	4.04	13.5	15	0.46
Slough Creek	November–December	2006	20	1043	346.28	12.06	7.00	13.40	67.76	0.10	0.02	1.22	9.6	13	0.32
Agate Creek	March	2007	16	601	291.69	20.07	10.00	18.70	109.41	0.25	0.03	4.95	16.8	12	0.56
Druid Peak	March	2007	7	1074	351.93	17.27	6.00	12.20	220.66	0.09	0.01	1.62	11.1	11	0.37
Hellroaring	November–December	2007	3	262	887.39	18.94	8.00	19.00	38.82	0.15	0.01	2.75	5.4	8	0.18
Leopold	November–December	2007	17	1419	119.75	32.70	19.00	38.00	22.51	0.25	0.01	8.19	19.2	19	0.64
Slough Creek	November–December	2007	4	524	155.55	17.91	4.00	9.20	26.08	0.28	0.01	5.07	17.4	8	0.58
Druid Peak	March	2008	13	1177	236.99	8.30	5.00	8.00	178.14	0.14	0.01	1.16	12.9	16	0.43
Druid Peak	November–December	2008	17	1556	236.99	8.30	5.00	8.00	49.83	0.14	0.01	1.16	8.7	16	0.29
Leopold	November–December	2008	11	822	270.99	12.63	6.00	14.00	29.80	0.34	0.01	4.29	12	16	0.40
Oxbow Creek	November–December	2008	29	840	162.27	10.48	5.50	14.20	32.94	0.27	0.03	2.84	11.4	17	0.38
Blacktail	March	2009	7	426	318.72	14.41	9.00	15.00	232.30	0.40	0.02	5.79	18	6	0.60
Druid Peak	March	2009	5	630	590.06	11.72	6.50	12.50	332.77	0.16	0.01	1.91	15	13	0.50
Everts	March	2009	11	523	88.71	19.85	10.50	17.30	179.11	0.45	0.02	8.95	6.6	6	0.22
Blacktail	November–December	2009	9	642	318.72	14.41	9.00	15.00	32.94	0.40	0.01	5.79	7.2	10	0.24
Druid Peak	November–December	2009	3	1235	590.06	11.72	6.50	12.50	56.27	0.16	0.00	1.91	3.9	13	0.13
Blacktail	March	2010	7	452	300.54	14.68	7.00	13.00	125.34	0.21	0.02	3.08	12.3	9	0.41
Lamar Canyon	March	2010	3	263	99.15	8.33	7.00	8.80	134.08	0.15	0.01	1.26	4.2	3	0.14
Silver	March	2010	5	998	471.14	11.32	6.50	10.10	162.02	0.09	0.01	1.06	4.2	5	0.14
Blacktail	November–December	2010	10	553	300.54	14.68	7.00	13.00	43.76	0.21	0.02	3.08	12.6	10	0.42
Druid Peak	November–December	2010	3	643	444.79	12.09	6.00	10.40	62.52	0.12	0.00	1.44	3.6	11	0.12
Agate Creek	March	2011	7	808	146.46	13.71	10.00	19.60	349.03	0.10	0.01	1.31	17.7	8	0.59
Blacktail	March	2011	6	446	538.31	16.68	12.00	23.20	329.28	0.22	0.01	3.62	22.2	12	0.74
Lamar Canyon	March	2011	24	1133	264.04	12.70	11.50	14.00	359.61	0.11	0.02	1.44	16.8	7	0.56
Agate Creek	November–December	2011	1	171	146.46	13.71	10.00	19.60	104.20	0.10	0.01	1.31	3.3	9	0.11
Blacktail	November–December	2011	19	718	538.31	16.68	12.00	23.20	101.32	0.22	0.03	3.62	15	15	0.50
Lamar Canyon	November–December	2011	6	471	264.04	12.70	11.50	14.00	79.39	0.11	0.01	1.44	8.7	7	0.29
Blacktail	March	2012	14	638	560.37	17.68	8.50	15.00	232.54	0.15	0.02	2.65	8.4	12	0.28
Agate Creek	November–December	2012	1	418	250.99	8.55	4.50	8.30	62.41	0.08	0.00	0.68	6.3	8	0.21
Blacktail	November–December	2012	5	722	560.37	17.68	8.50	15.00	61.27	0.15	0.01	2.65	8.7	15	0.29
Lamar Canyon	November–December	2012	12	1165	415.57	11.33	9.00	14.60	60.13	0.01	0.01	0.08	5.7	11	0.19

^aStudy represents the observation session with November–December representing early winter and March representing late winter.

^bTIV travel is the total amount of time the pack was observed traveling not associated with a kill.

^cTerritory size was calculated using 90% isopleths of kernel density.

^dMean SWE is the average snow water equivalent within a pack's territory.

^eEstimated kills is calculated by multiplying the index of elk kills per day by the total number of days in the study period (30).

^fIndex of elk kills per day is calculated using an index method that characterized the number of elk kills per wolf pack per index day. The number of elk kills is the total number of elk kills found by the ground or aerial crews, which is divided by the number of days the wolf pack was visually observed from the ground or radio or visually located by the aircraft.

Table 2. Mean seasonal yearly wolf (*Canis lupus*) pack encounter rates with elk (*Cervus elaphus*) on the Northern Range of Yellowstone National Park, winter years 2004–2012, using the total number of observed wolf–elk encounters and total amount of time wolves were observed searching for prey.

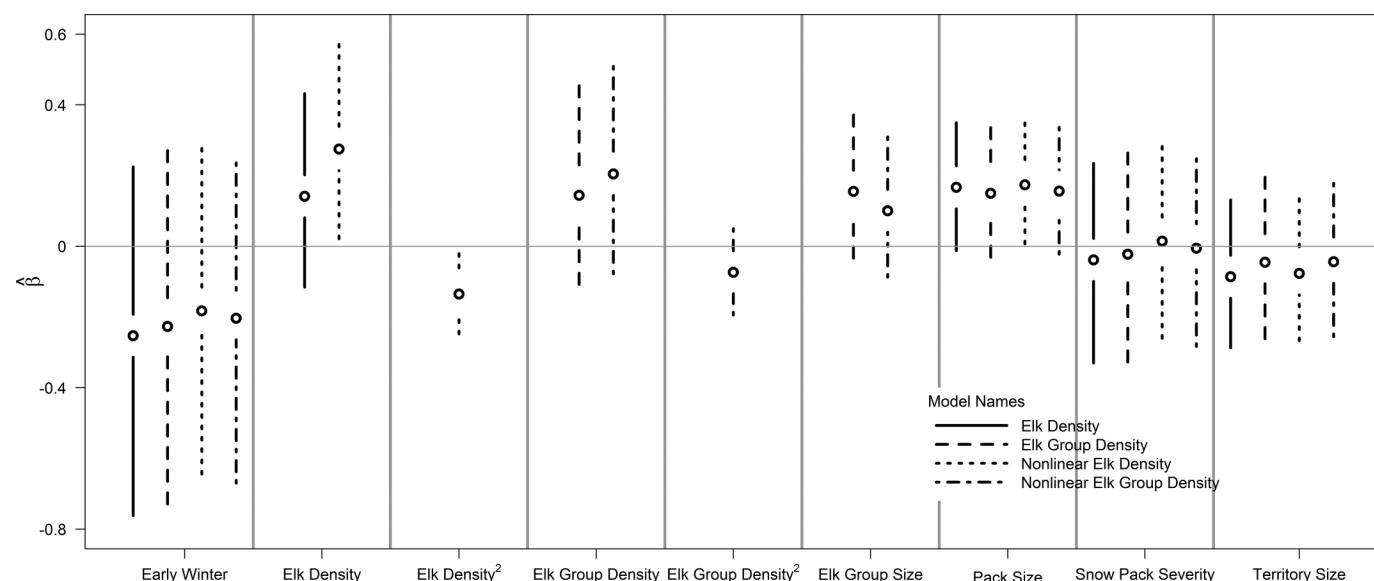
Winter year ^b	Early winter ^a					Late winter ^a				
	Elk encounters	Hours	Encounter rate	Lower CI ^c	Upper CI	Elk encounters	Hours	Encounter rate	Lower CI	Upper CI
2004	49	46.3	1.1	0.8	1.4	42	36.7	1.1	0.8	1.5
2005	33	42.7	0.8	0.5	1.1	57	54.0	1.1	0.8	1.4
2006	42	32.8	1.3	0.9	1.7	54	51.6	1.0	0.8	1.4
2007	24	36.8	0.7	0.4	1.0	23	27.9	0.8	0.5	1.2
2008	57	53.6	1.1	0.8	1.4	13	19.6	0.7	0.4	1.1
2009	12	31.3	0.4	0.2	0.7	23	26.3	0.9	0.6	1.3
2010	13	19.9	0.7	0.3	1.1	15	28.6	0.5	0.3	0.9
2011	26	22.7	1.1	0.7	1.7	37	39.8	0.9	0.7	1.3
2012	18	38.4	0.5	0.3	0.7	14	10.6	1.3	0.7	2.2

^aWinter year starts in October and ends the following September, taking the name of the year in which the majority of the months fall within. For example, the calendar year November 2010 is in the winter year 2011.

^bEncounter rate is calculated as the number of wolf–elk encounters per hour of observed traveling.

^cConfidence intervals were calculated using exact Poisson confidence intervals (Cohen and Yang 1994).

Fig. 2. Estimated coefficients and 95% credible intervals of the models hypothesized to predict wolf (*Canis lupus*) – elk (*Cervus elaphus*) encounter rates on the Northern Range of Yellowstone National Park (winter years 2004–2012).



winter pack territory size (mean = 310.34 km², SD = 162.54) and pack size (mean = 11.87, SD = 4.77) to characterize wolf pack space use and prey detectability.

Results

Average wolf–elk encounter rates in early winter (mean = 0.79 encounter/h traveling, SD = 0.46) were lower than encounter rates in late winter (mean = 0.94 encounter/h traveling, SD = 0.33) (Table 2). However, after accounting for other covariates, the difference between early and late winter encounter rates was not statistically significant (Fig. 2).

The sign of the estimated coefficients agreed with the hypothesized effects except for SWE. Coefficients associated with elk density, elk group density, group size, and pack size were all positive; regression coefficients associated with territory size and SWE were negative (Fig. 2). However, the 95% credible intervals for all coefficients were fairly wide and included 0, most likely due to weak effects and our small sample ($n = 46$ pack study periods). Despite this limitation, season, pack size, SWE, and territory size were all robust to how elk abundance was modeled (elk density, group density; linear or nonlinear relationship with encounter rates) (Fig. 2). The effect of elk group size was also robust to the methods

used to describe them (average, median, and 70th percentile), but using the median and 70th percentile reduced the effect of group density in the models (Table 3).

There was a significant curvilinear relationship between elk density and encounter rates (Fig. 3) but not between elk group density and encounter rates (Fig. 2). We further explored the elk density relationship using a single linear spline to estimate the elk density that satiates encounter rates (Fig. 4). Encounter rates maximized at a density of 3.27 elk/km² (95% CI = 1.59, 5.94). Unexplained year-to-year variability in encounter rates was minimal, and all credible intervals of the posterior distributions of the random effect of year overlapped 0 (Fig. 5).

Wolf pack encounter rates (elk groups encountered per hour of observed wolf traveling) and the estimated number of elk killed in early winter were related (adjusted $r^2 = 0.25$, $p = 0.013$) but not in late winter (adjusted $r^2 = 0.009$, $p = 0.67$) (Fig. 6).

Discussion

The nonlinear effect of elk density on encounter rate is a mechanism that may generate the asymptote associated with a Type II or Type III functional response. This, along with previous work that did not detect prey switching (Tallian et al. 2017), suggests a

Table 3. Coefficient estimates and 95% credible intervals of parameters from the Bayesian models of wolf (*Canis lupus*) – elk (*Cervus elaphus*) encounter rates on the Northern Range of Yellowstone National Park, winter years 2004–2012.
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Model parameter ^a	Elk density model						Nonlinear elk group density model						Nonlinear elk group density median group size model ^b						Nonlinear elk group density 70th percentile group size model ^b						Asymptotic elk density model					
	Elk group density model			Estimate BCI ^c			Nonlinear elk group density model			Estimate BCI			Nonlinear elk group density median group size model ^b			Estimate BCI			Nonlinear elk group density 70th percentile group size model ^b			Estimate BCI			Asymptotic elk density model					
	Estimate	BCI ^c	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	Elk density	Estimate	BCI	
Pack size	0.17	-0.01, 0.35	0.15	-0.03, 0.34	0.16	-0.02, 0.34	0.17	0.01, 0.35	0.17	0.00, 0.36	0.17	0.00, 0.35	0.19	-0.22	0.02, 0.36	-0.83, 0.75	0.81	0.17, 1.85												
Critical elk density																														
Elk density	0.14	-0.12, 0.43																												
Elk density ²																														
Elk group size average																														
Elk group size median																														
Elk group size																														
70th percentile																														
Elk group density																														
Elk group density ²																														
Territory size	-0.09	-0.29, 0.13	-0.05	-0.26, 0.20	-0.04	-0.26, 0.18	-0.08	-0.27, 0.13	-0.01	-0.28, 0.28	-0.07	-0.27, 0.14	-0.09	-0.28, 0.11																
SWE ^d	-0.04	-0.33, 0.23	-0.02	-0.33, 0.26	-0.01	-0.28, 0.25	0.01	-0.26, 0.28	0.04	-0.12, 0.22	0.01	-0.27, 0.29	0.03	-0.25, 0.29																
Early winter ^e	-0.25	-0.76, 0.22	-0.23	-0.73, 0.27	-0.20	-0.67, 0.24	-0.18	-0.64, 0.28	-0.22	-0.68, 0.27	-0.18	-0.67, 0.32	-0.16	-0.62, 0.30																
Intercept	-4.11	-4.54, -3.68	-4.13	-4.57, -3.67	-4.07	-4.51, -3.63	-4.02	-4.43, -3.60	-4.05	-4.49, -3.61	-4.06	-4.48, -3.64	-3.68	-4.48, -3.64																

^aParameter estimates are from variables centered and scaled using mean and standard deviation.

^bModels used to assess the sensitivity of different measures of elk herd size on encounter rate.

^cBayesian credible intervals from the 2.5 and 97.5 quantiles of the posterior distribution.

^dSWE variable is the average daily snow water equivalent during the study.

Type II functional response in this primarily wolf–elk system. However, the observed use of alternative prey through scavenging on bison that occurs at lower elk densities (Tallian et al. 2017) could promote a Type III functional response, since scavenging may act to maintain lower kill rates than expected. Regardless, our work suggests that the asymptote of the functional response in either of these cases may be at least partially driven by the nonlinear effect of elk density on encounter rate.

Other studies have shown that at low prey densities, kill rates increase proportionally with prey density (Dale et al. 1994; Messier 1994; Hayes et al. 2000; Messier and Joly 2000). Likewise, visual assessment of the prediction curves suggests that at low prey densities, there is a near-linear relationship between encounter rate and elk density, which could lead to the linear relationship between kill rate and prey density found in other low-density systems (Figs. 3 and 4). However, the nonlinear relationship that we found at high densities suggests that encounter rates may be affected by elk group formation and (or) may be limited by the amount of time required to evaluate and target elk during an encounter (MacNulty et al. 2007).

Small samples at low prey densities make it difficult to determine the exact relationship between encounter rate and elk density at lower elk densities (Marshal and Boutin 1999). Thus, we were not able to determine if the relationship was truly linear at lower elk densities or test whether a Type II or Type III functional response provides a better fit to the data. In addition, a variety of other factors influence the year-to-year variability in encounter rates, which makes it difficult to determine the form of the functional response when data are limited.

We hypothesized that the factors that affect encounter rates and kill rates in other wolf–ungulate systems would all influence wolf–elk encounter rates on the NR of YNP. However, we did not find convincing evidence that factors affecting kill rates in this system (wolf pack size, snow, and season) influence encounter rates (Fig. 2). This suggests that the mechanism by which these factors influence kill rate is through hunting success given that kill rate is a product of encounter and success rates.

We hypothesized that snowpack severity (indexed by SWE) would reduce elk movement, increase elk concentration, make elk location more predictable, and increase encounter rates. This hypothesis was not supported despite winter severity and snow depth being a primary driver of wolf kill rate in YNP and other wolf–ungulate systems (Mech et al. 1971, 1998, 2001; Peterson 1977; Nelson and Mech 1986; Smith et al. 2004). Elk avoid deep snow, causing them to concentrate in areas with less snow (Sweeney and Sweeney 1984; Eriksen et al. 2009). Additionally, elk winter home range sizes increase with mean SWE (Anderson et al. 2005), suggesting that under some conditions, elk locations where snow is deep may be less predictable (but see Rivrud et al. 2010).

Snow depth most often influences success of an encounter when prey run into deep snow and our results suggest that snow depth has a stronger effect on the success rate than on encounter rate (Mech et al. 2015). Thus, if snowpack severity does limit elk movements, snowpack severity had a stronger effect on success of encounters than on their occurrence. Further information on the effect of snowpack on elk home ranges in mountainous habitats is needed to better understand the relationship between snow depth and elk movement.

Although not statistically significant, wolf encounter rates of elk were lower in early winter than in late winter, aligning with trends in kill rate (Smith et al. 2004; Metz et al. 2012). Increased kill rates in late winter have been attributed to a decline in elk condition throughout winter caused by limited food, thermoregulation costs, and gestation that reduce fat reserves (DelGiudice et al. 1991; Metz et al. 2012). Thus, increased kill rates in late winter may be due to killing success as well as to an increase in encounter rates.

Wolf pack size had a positive, although not statistically significant, effect on encounter rates as hypothesized (Fig. 2). The prob-

Fig. 3. Prediction curve and 95% credible intervals of the nonlinear elk density model on wolf (*Canis lupus*) – elk (*Cervus elaphus*) encounter rates at varying levels of elk density on the Northern Range of Yellowstone National Park (winter years 2004–2012).

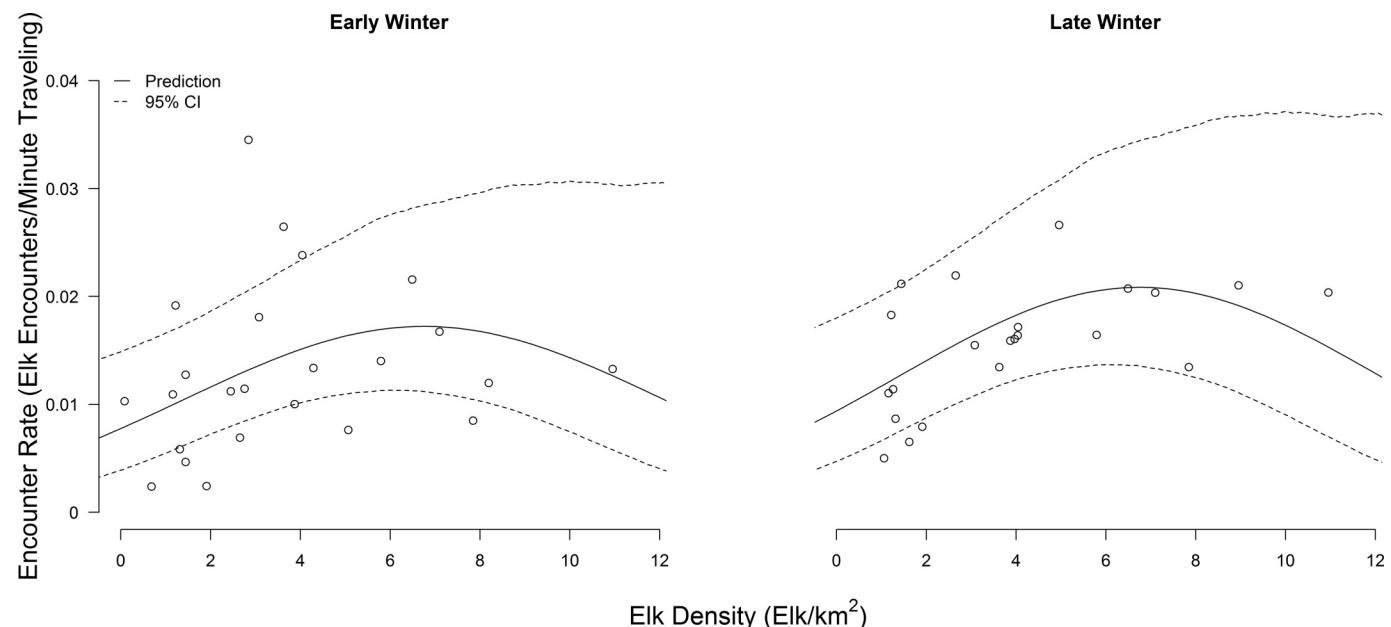
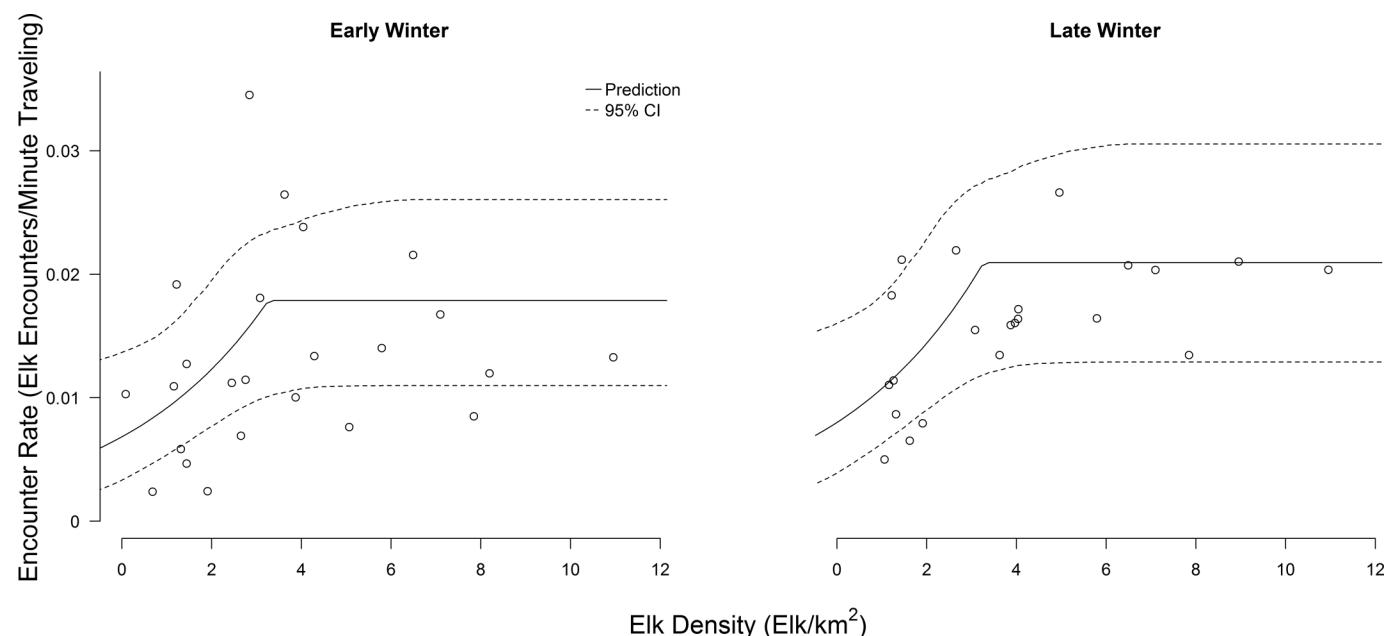


Fig. 4. Prediction curve and 95% credible intervals of the asymptotic elk density model on wolf (*Canis lupus*) – elk (*Cervus elaphus*) encounter rates at varying levels of elk density on the Northern Range of Yellowstone National Park (winter years 2004–2012).



ability of wolves killing elk does not increase in hunting groups larger than four (MacNulty et al. 2012). Nonetheless, our results suggest that larger wolf packs may encounter more elk, perhaps because of a larger search radius or greater motivation of individuals to encounter prey, since there is a negative relationship between biomass acquisition and pack size (Metz et al. 2012). Such an advantage could reduce the wolf freeloading burden (MacNulty et al. 2012) and partly explain the positive effect associated with living in larger packs. Furthermore, packs sometimes split temporarily, hunting as smaller and more efficient groups (Mech 1966; Metz et al. 2011). These smaller hunting groups within large packs and with larger search radii may explain the higher encounter rates in larger packs. Moreover, we may have underestimated

encounter rates for large packs because of their increased tendency to forage separately (Metz et al. 2011). Pack size is highly dependent on the timing of dispersal of maturing members, triggered by competition for food and mates (Mech and Boitani 2003). Packs experience increased dispersal and reduced sizes in years of low food availability (Messier 1985; Peterson and Page 1988). High encounter rates might reflect more food, so individual wolves postpone dispersal, leading to larger packs (Mech et al. 1998). Therefore, it might be difficult to sort out cause and effect between more food, encounter rates, and pack size.

Pack size was used as a proxy for the search radius of a traveling pack and winter territory size for pack space use. We found no significant relationship between wolf pack territory size and en-

Fig. 5. Mean and 95% credible intervals of the posterior distribution of the random year effect describing year-to-year variation of wolf (*Canis lupus*) – elk (*Cervus elaphus*) encounter rates on the Northern Range of Yellowstone National Park (winter years 2004–2012) not accounted for by the other parameters within the nonlinear elk density model.

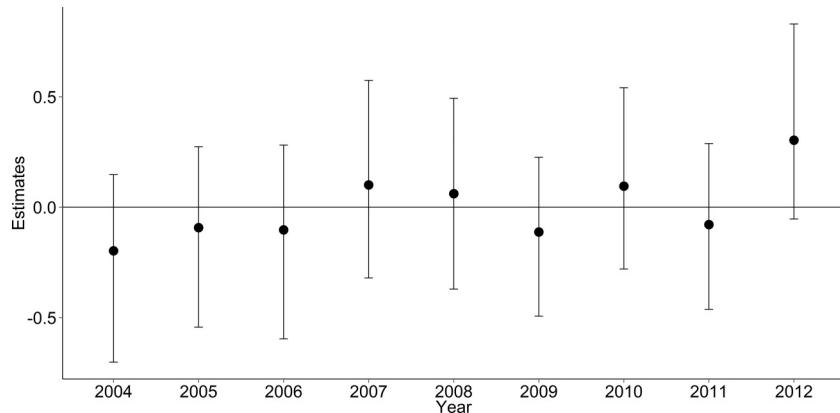
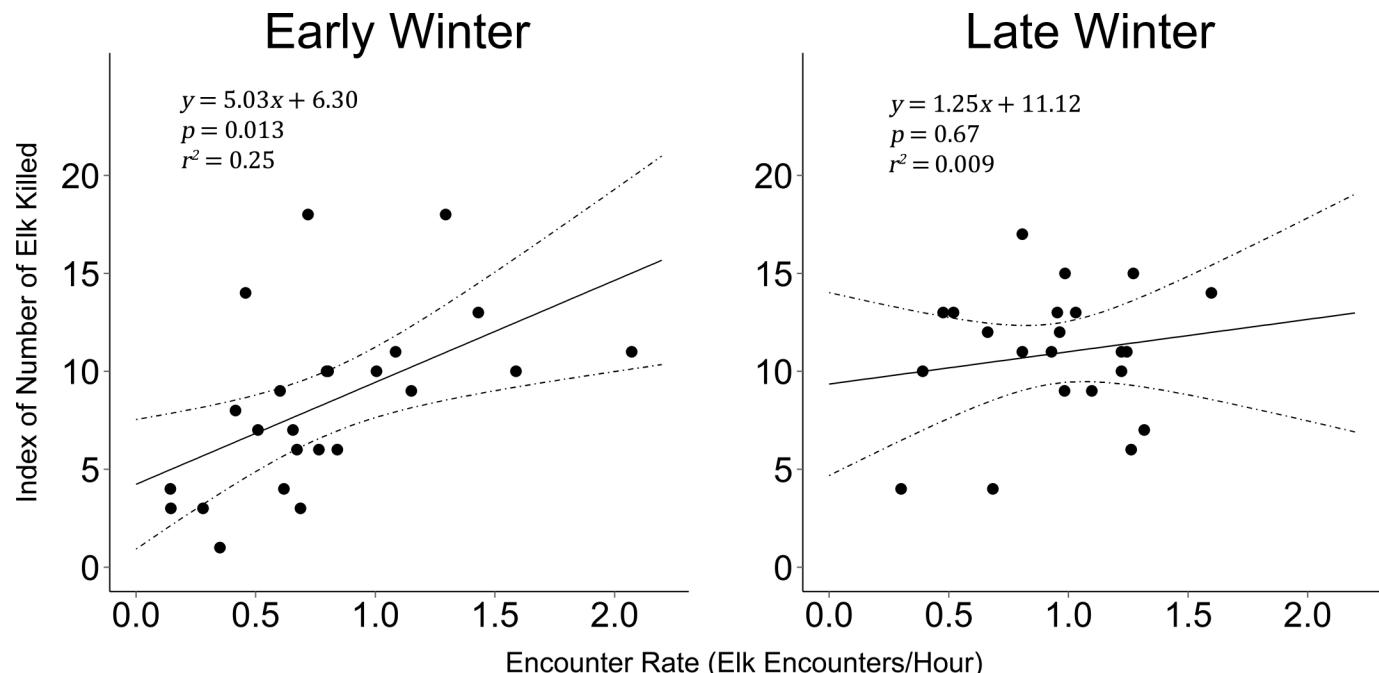


Fig. 6. Linear regression line and 95% confidence intervals of the effect of hourly wolf (*Canis lupus*) – elk (*Cervus elaphus*) encounter rates when searching for prey on the number of elk killed during early (15 November – 15 December) and late (1–30 March) winter on the Northern Range of Yellowstone National Park, winter years 2004–2012.



counter rate of elk. Wolf pack territory size might depend on landscape features and the arrangement of prey on the landscape but might not accurately reflect prey availability or distribution during different seasons. Territory size is often correlated with prey biomass (Fuller et al. 2003; Schmidt et al. 2007), as it was in this study ($r = -0.35$, $p = 0.02$), but is also constrained by neighboring packs. Due to our limited sample of locations defining pack territory size, winter territory sizes may not have accurately represented the space use of wolves during our 30 day study sessions.

In other large carnivore studies, group density was a better predictor of encounter rates and kill rate than was total density because only one animal is usually taken from a group (Huggard 1993; Fryxell et al. 2007; McLellan et al. 2010). Prey grouping creates a space void of prey that would be filled if individuals were randomly or evenly distributed on the landscape. Elk group size is correlated with elk density, so despite increases in population, the number and distance between elk groups might remain the same,

which could lead to a lower encounter rate than expected with randomly distributed elk. The coarseness of our elk group density data might have damped the relationship that we found because constancy in elk group composition is low, with individuals changing grouping strategies depending on habitat type, predation risk, snow depth, and season (Knight 1970; White et al. 2011). Another reason we did not find an effect of elk group density is that both it and elk group size are functions of elk density ($r = 0.90$, $p < 0.001$ and $r = 0.75$, $p < 0.001$, respectively).

Many of the factors that explain variation in wolf kill rates of elk were seemingly unrelated to encounter rates, which raises the question of how encounter rates influence wolf kill rates. Encounter rates were correlated with the number of elk killed in early (but not late) winter. Differences in success rates (probability of a kill, given an encounter) during early and late winter may help to explain this result. Success rates in early winter likely vary little across years due to the abundance of calves on the landscape and their inherent vulnerability (Metz et al. 2012). By contrast, more

adults appear in the diet in late winter, with year-to-year variability in success rates likely driven by snow and the decline in the overall nutritional condition of the herd (Mech et al. 2001; Cook et al. 2004; Metz et al. 2012). This additional variability in success rates during late winter may dampen the strength of the relationship between encounter and kill rates.

The lack of a significant effect of SWE, territory size, and season suggests that wolves behaviorally compensate in response to changes in these factors to maintain encounter rates. Wolves may change the speed of travel, directional persistence, and amount of time spent searching for prey to compensate for changes in prey abundance, predictability, and movement. Additionally, wolves may adapt hunting strategies to take advantage of elk in poor condition or near vulnerable landscape features, i.e., terrain traps (Mech et al. 2015). Our study assumed that all observed search behavior contributed equally to the probability of an encounter and that all encounters contributed equally to hunting success; however, this may not always be the case. Huggard (1993) proposed that a pack's search time between kills would not decline as significantly as predicted at high kill rates because most kills occur in distinct, predictable areas, and the distances between these kill locations remain the same regardless of wolves encountering prey in other unpredictable locations. In our study area, elk kills are similarly found in predictable locations, suggesting a similar mechanism (Kauffman et al. 2007). Other predators change searching behavior and rate when experiencing low encounter rates to locate prey more efficiently (Biesinger and Haefner 2005; Travis and Palmer 2005; Ioannou et al. 2008). For example, wolves with lower encounter rates may make longer, more extensive movements to detect prey.

The speed at which wolves travel depends on their activity, and normal travel speeds are between 8 and 9 km/h when hunting (Burkholder 1959; Mech 1966, 1994; Shelton 1966). The average speed of wolf packs in this study was 3.61 km/h ($SD = 0.87$, range = 1.98–6.20 km/h), which is similar to other studies of wolf travel speeds (Musiani et al. 1998). We know of no studies that compare daily travel rates and prey type or density, but these factors might affect both wolf travel rate and the distance wolves cover. Such behavior variation might compensate for variations in encounter rates. Wolves do travel at different rates in different areas. In winter on Isle Royale, wolves traveled an average of 14.4 km/day (Mech 1966), in Poland 22.8 km/day (Jedrzejewski et al. 2001), and in Italy 27.4 km/day (Ciucci et al. 1997). At these rates of travel, we would expect wolves to encounter elk from three to seven times per day using the range of average travel distances above, average speed of wolves from this study, and the average encounter rate in early and late winter.

Additional studies of wolf hunting behavior might further our understanding of how wolves compensate for variations in the above-discussed factors to maintain encounter rates and for changes in elk density to maintain hunting success. Such studies should focus on how wolves adjust their hunting behavior to maintain adequate prey encounter rates despite the many other factors that could affect those rates.

Conclusion

We found a nonlinear relationship between elk density and wolf–elk encounter rates, which suggests a possible mechanism for generating the asymptote associated with both Type II and Type III functional responses. The correlation between encounter rate and kill rate in early winter provides additional support for encounter rate being a mechanism behind the functional response. These results support theoretical models of kill rate but also reemphasize the stochastic effect that weather and season have in temperate systems and the potential for wolves to behaviorally compensate in response to changes in these factors to maintain encounter rates and kill rates.

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