

In the format provided by the authors and unedited.

Predation shapes the evolutionary traits of cervid weapons

Matthew C. Metz ^{1,2*}, Douglas J. Emlen³, Daniel R. Stahler², Daniel R. MacNulty⁴, Douglas W. Smith² and Mark Hebblewhite ¹

¹Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA. ²Yellowstone Wolf Project, Yellowstone Center for Resources, Yellowstone National Park, WY, USA. ³Division of Biological Sciences, University of Montana, Missoula, MT, USA. ⁴Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT, USA.
*e-mail: matthew.metz@umontana.edu

Predation shapes the evolutionary traits of cervid weapons

Matthew C. Metz^{1,2*}, Douglas J. Emlen³, Daniel R. Stahler², Daniel R. MacNulty⁴,
Douglas W. Smith², Mark Hebblewhite¹

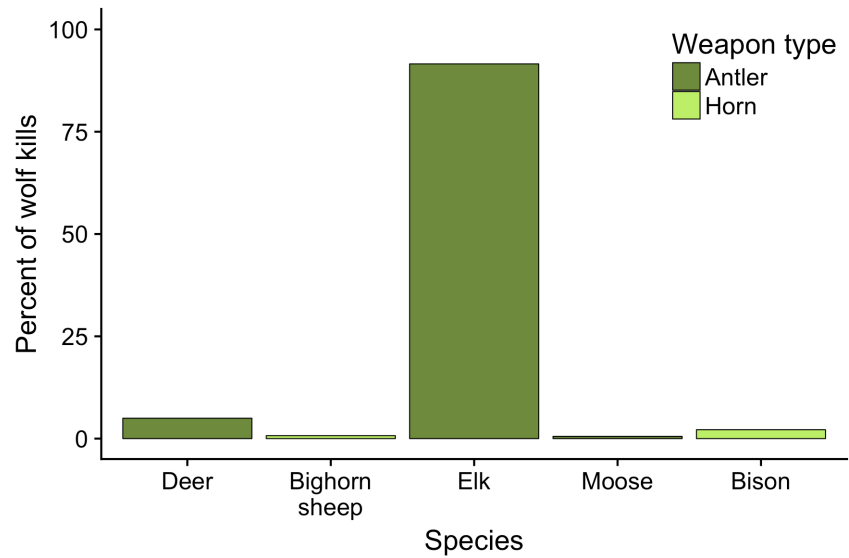
¹Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA

²Yellowstone Wolf Project, Yellowstone Center for Resources, Yellowstone National Park, WY, USA

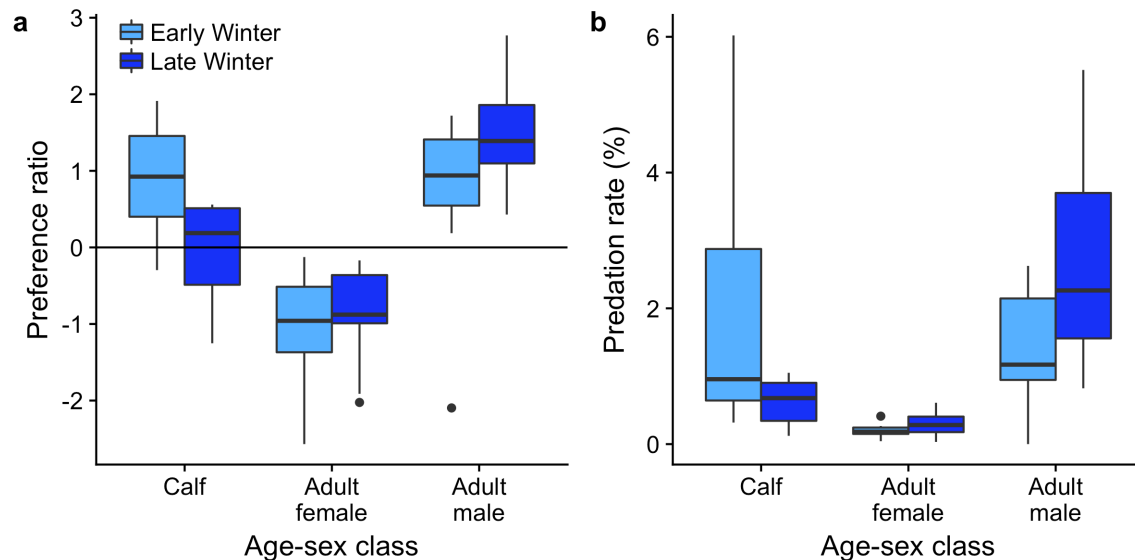
³Division of Biological Sciences, University of Montana, Missoula, MT, USA

⁴Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT, USA

*email: matthew.metz@umontana.edu

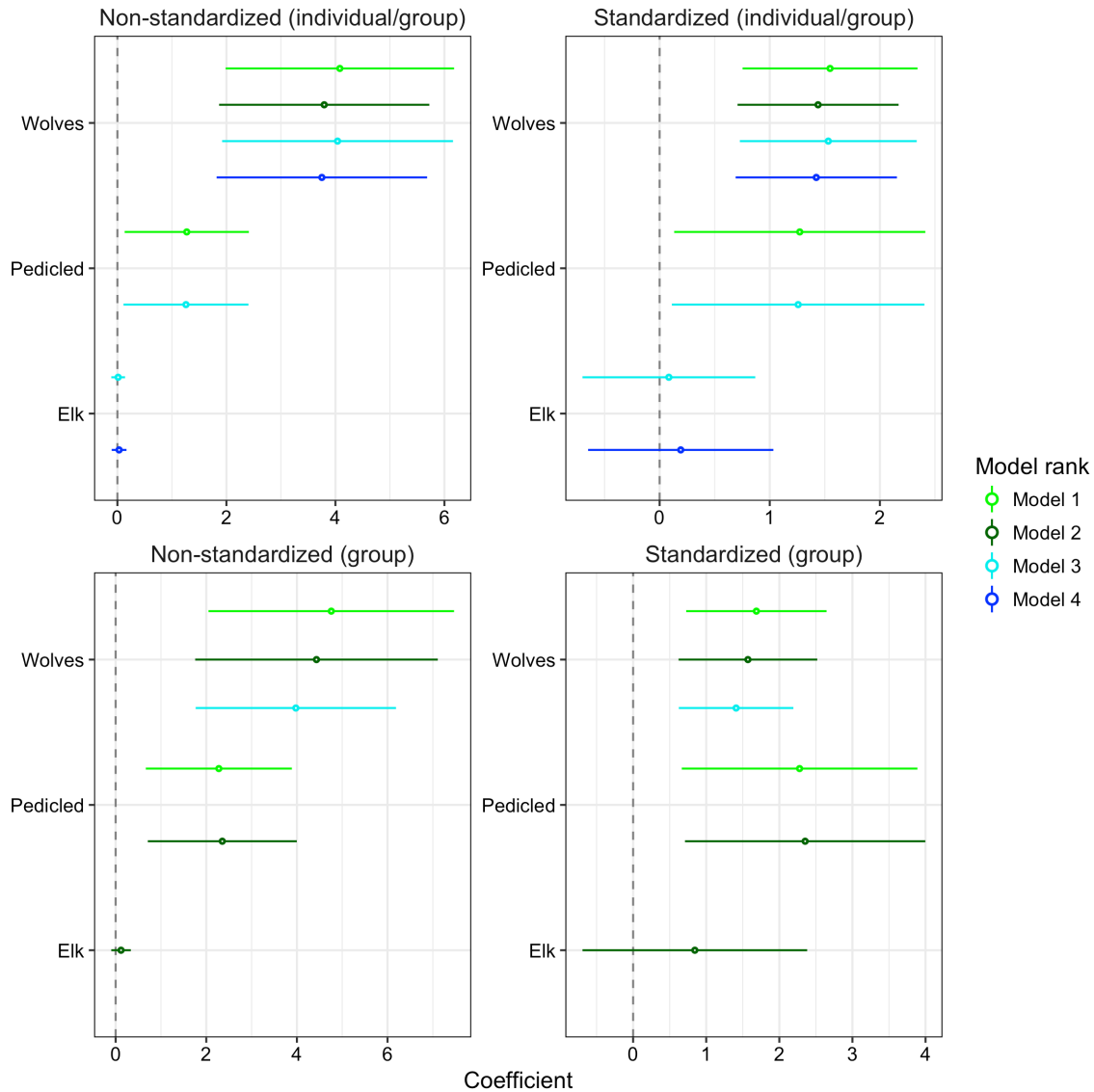


Supplementary Figure 1. Percent of wolf-killed ungulates in northern Yellowstone during winter. Percent of each species calculated from 1,104 wolf-killed ungulates detected during 30-day early (mid-November to mid-December) and late (March) winter monitoring periods from November 2003 – March 2016.

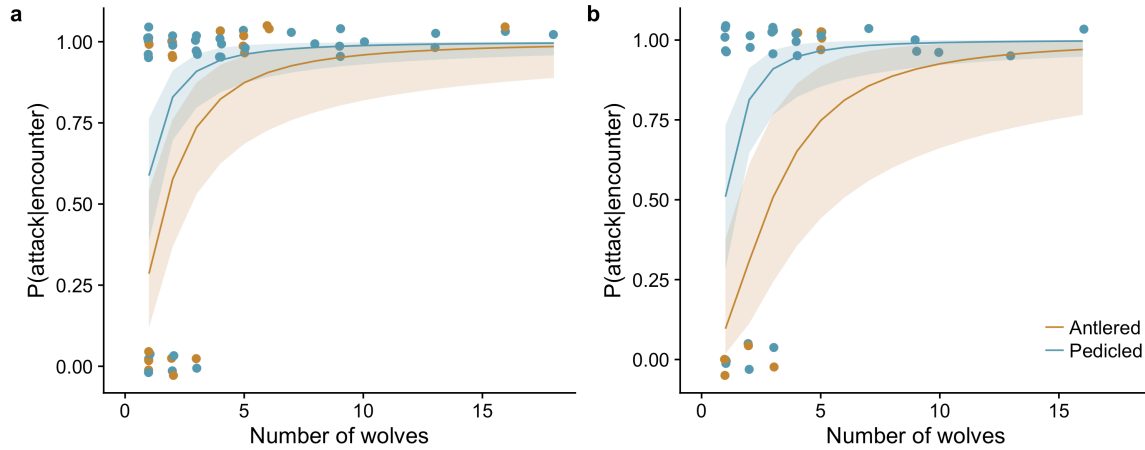


Supplementary Figure 2. Wolf preference ratio and predation rate in northern

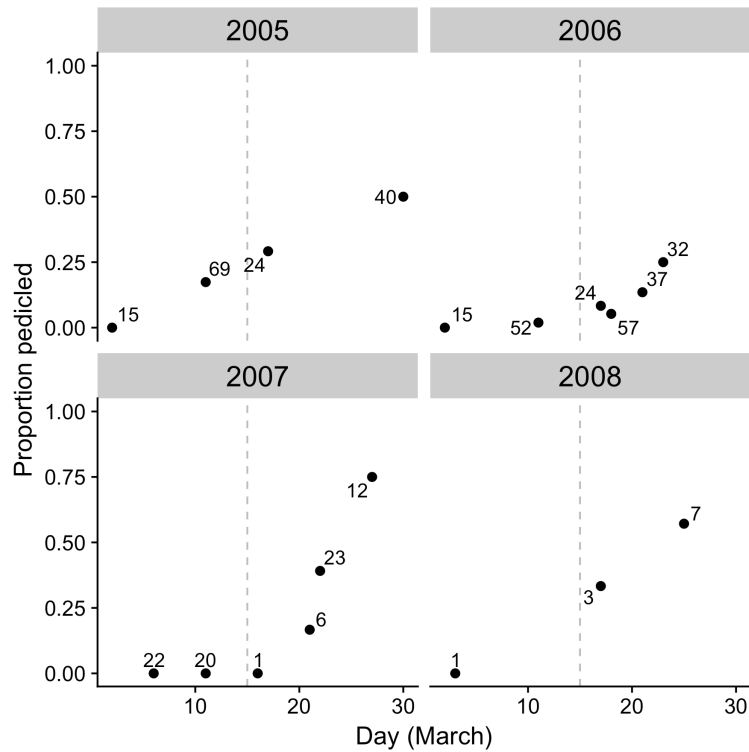
Yellowstone. a, Wolf preference ratio (equation (1) in *Methods*) for elk calves, adult females, and adult males. **b,** Wolf predation rate on elk calves, adult females, and adult males (number of age-sex specific kills divided by age-sex specific elk abundance). Each panel displays a box plot of annual estimates from 30-day study periods¹, November 2003 – March 2016 (no estimates for four years because elk age-sex surveys did not occur). Wolf predation statistics use data about wolf kill composition and kill rate from three wolf packs that were intensively monitored by aerial and ground-based observations during each study period ($n = 14$ total packs)². These wolf predation statistics include only wolf kills detected by aerial and ground-based observations and do not correct for variation in detection probability among wolf kills of differing size^{2,3}. Wolf abundance estimates are for resident northern Yellowstone National Park wolves during early and late winter. Total elk abundance was estimated as described in *Methods*⁴, while the age-sex composition of the elk population was determined during a late winter population-wide survey conducted by the Northern Yellowstone Cooperative Wildlife Working Group¹. The specific equation used in panel **b** was *total northern YNP wolf abundance x wolf kill rate on elk x proportion age-sex class among detected wolf-killed elk*, divided by *abundance of age-sex class elk for northern Yellowstone*. The box plots display the median, as well as the first and third quartiles. Whiskers extend from the inter-quartile range to the largest value that is no further than $1.5 \times$ inter-quartile range, in each direction. Filled circles represent outliers.



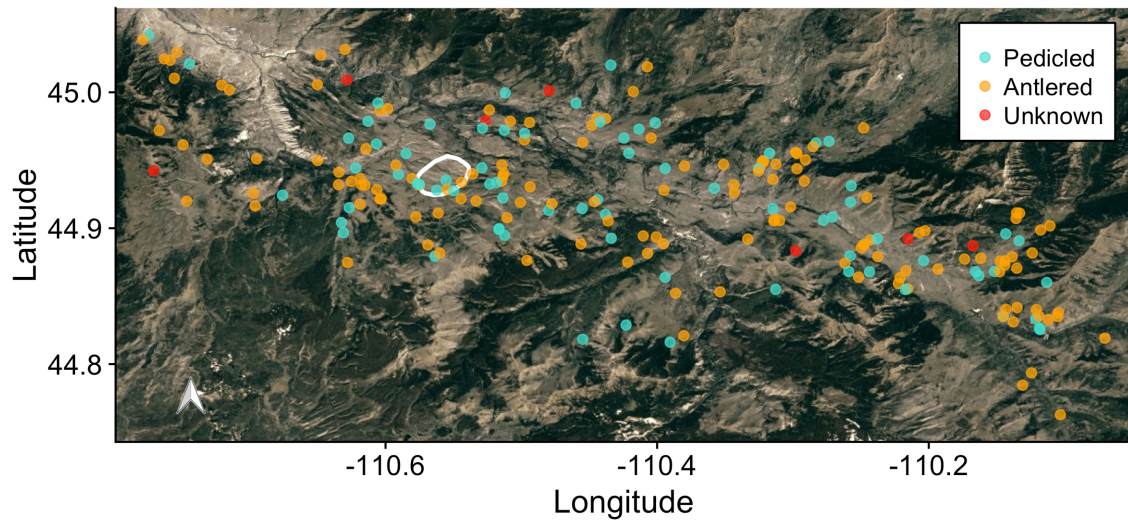
Supplementary Figure 3. Beta coefficients for top models describing factors affecting the probability of attack given an encounter with male elk. ‘Wolves’ represents wolf group size (log transformed), ‘Pedicled’ represents whether a pedicled individual(s) was present, and ‘Elk’ represents the number of elk. Panels display either non-standardized or standardized beta coefficients for models describing the likelihood that an encounter with solitary or ≥ 2 adult male elk included an attack (top row) and an encounter with ≥ 2 adult male elk included an attack (bottom row). Coefficients are displayed for models within 4 ΔAIC_c units of the top model (Supplementary Table 1). Error bars represent 85% confidence intervals. Model numbers identifying each model represent the model rank from Supplementary Table 1.



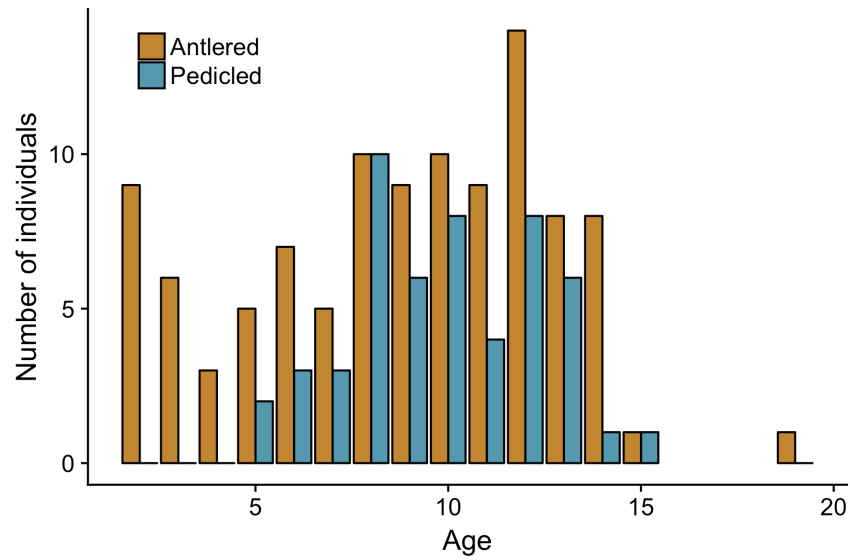
Supplementary Figure 4. Predictions for top models describing factors affecting the probability of attack given an encounter with male elk. Panels display predictions for the top model (Supplementary Table 1) describing the probability that wolves **a**, attacked solitary or groups of ≥ 2 adult male elk, and **b**, attacked groups of ≥ 2 adult male elk only. Shaded areas represent 85% confidence intervals.



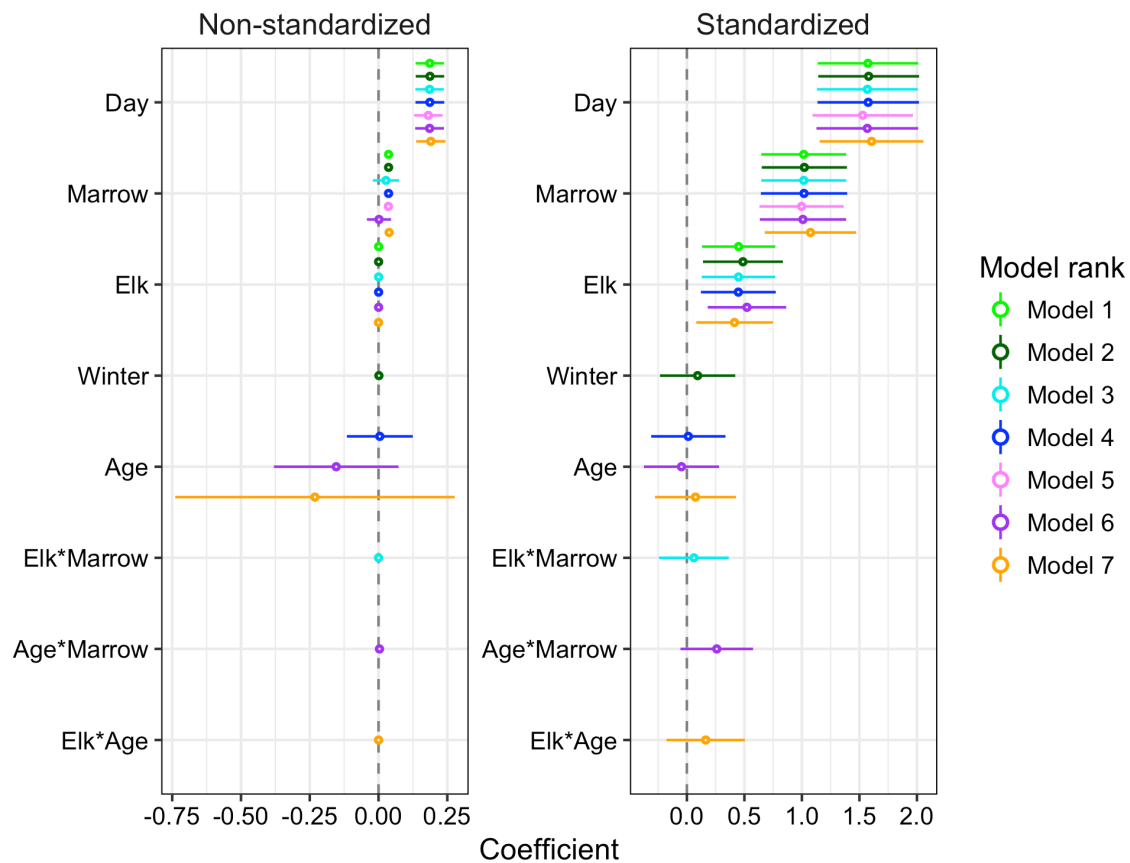
Supplementary Figure 5. Proportion of male elk that had cast their antlers during each male elk antler classification survey (2005 – 2008). Numbers indicate the number of individual male elk classified as pedicled or antlered during each survey. Dashed gray lines indicate the mid-point of the month that distinguishes ‘Early March’ from ‘Late March’.



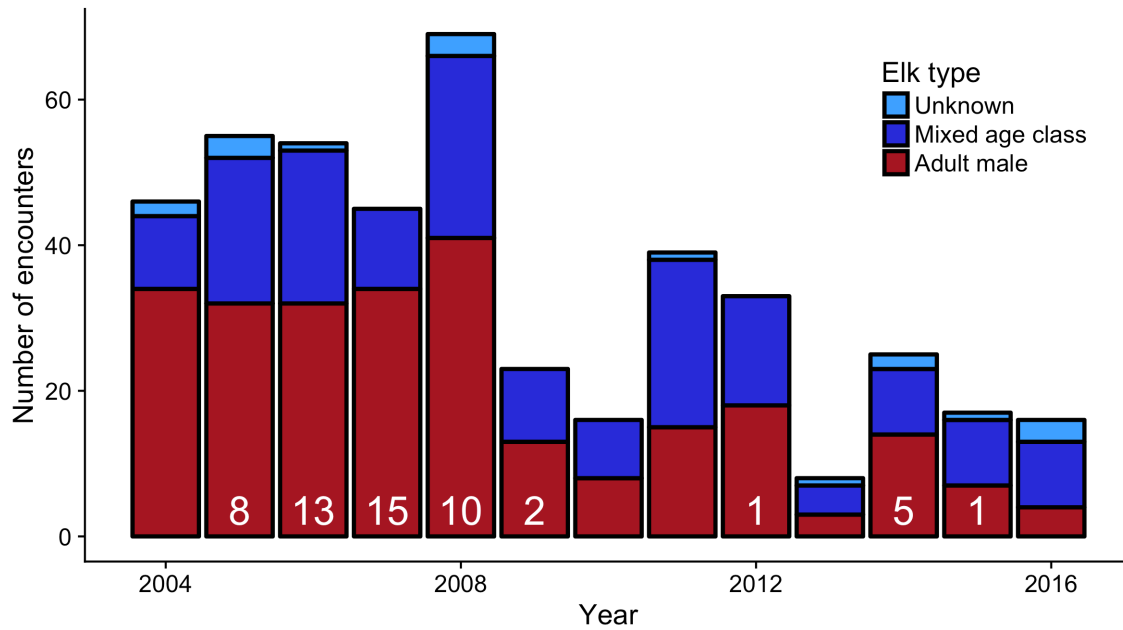
Supplementary Figure 6. Geographic distribution of 223 wolf-killed adult male elk detected during March (2004 – 2016). The white-lined polygon represents the 6.7 km² male elk classification survey unit (Supplementary Fig. 5).



Supplementary Figure 7. Age of wolf-killed adult male elk during March (2004 – 2016). Ages are displayed for the 157 individuals where we determined both the individual's age and nutritional condition.



Supplementary Figure 8. Beta coefficients for top models describing factors affecting the probability of a wolf-killed adult male elk (≥ 5 years old) being a pedicled individual. ‘Day’ represents the day in March, ‘Marrow’ represents elk femur marrow percent fat, ‘Elk’ represents elk abundance, ‘Winter’ represents winter severity, and ‘Age’ represents the elk’s age. Non-standardized and standardized beta coefficients are displayed for models within 4 ΔAIC_c units of the top model (Supplementary Table 3). Error bars represent 85% confidence intervals. Model numbers identifying each model represent the model rank from Supplementary Table 3.



Supplementary Figure 9. Number of observations of wolf-elk encounters during March (2004 – 2016). White numbers indicate the number of encounters included in our analysis of how the presence of pedicled individual(s) affected the probability of wolves attacking male elk.

a, Probability of attack given an encounter with male elk (groups or solitary animals)

Model	K	LL	AICc	ΔAICc	w_i
(1) pedicled + wolves	3	-21.63	49.72	0.00	0.42
(2) wolves	2	-22.97	50.17	0.45	0.33
(3) pedicled + wolves + elk	4	-21.61	52.03	2.30	0.13
(4) wolves + elk	3	-22.91	52.29	2.57	0.12

b, Probability of attack given an encounter with groups of ≥ 2 male elk

Model	K	LL	AICc	ΔAICc	w_i
(1) pedicled + wolves	3	-14.41	35.54	0.00	0.52
(2) pedicled + wolves + elk	4	-13.89	37.03	1.49	0.25
(3) wolves	2	-16.92	38.18	2.65	0.14
(4) wolves + elk	3	-16.44	39.61	4.07	0.07

Supplementary Table 1. Model selection results of factors affecting the probability of attack given an encounter with male elk. We evaluated the effects of log-transformed wolf group size (wolves), the number of elk (elk), and whether elk groups contained pedicled individual(s) (pedicled). Panels identify the top models describing the probability that **a**, an encounter would include an attack for encounters with solitary or ≥ 2 adult male elk, and **b**, an encounter would include an attack for only encounters with ≥ 2 male elk. Models with a Δ AIC_c < 6 are displayed. Our ability to differentiate among the top models was limited by our relatively small sample size. Nonetheless, the number of wolves (wolves) and whether or not a pedicled individual was present (pedicled) were in the top model for **a** and **b**. See Supplementary Fig. 3 for non-standardized and standardized beta coefficient estimates for models within 4 Δ AIC_c units of the top model.

Year	Unknown	Pedicated	One Antler	Antlered
2004	3	4	0	18
2005	1	18	0	10
2006	0	1	0	12
2007	0	7	1	17
2008	1	12	1	20
2009	1	10	0	14
2010	0	2	0	10
2011	0	3	0	6
2012	0	4	1	8
2013	0	0	0	5
2014	1	2	0	4
2015	0	5	0	11
2016	0	4	0	6

Supplementary Table 2. Antler condition for 223 wolf-killed adult male elk (2004 – 2016).

Model	K	LL	AICc	$\Delta AICc$	w_i
day + marrow + elk	4	-65.04	138.38	0.00	0.25
day + marrow + elk + winter	5	-64.96	140.36	1.98	0.09
elk * marrow + day	5	-65.00	140.45	2.07	0.09
day + marrow + elk + age	5	-65.04	140.53	2.15	0.09
day + marrow	3	-67.22	140.61	2.23	0.08
age * marrow + day + elk	6	-64.33	141.29	2.91	0.06
elk * age + day + marrow	6	-64.80	142.23	3.85	0.04
winter * marrow + day + elk	6	-64.90	142.44	4.06	0.03
elk * marrow + day + winter	6	-64.93	142.50	4.11	0.03
day + marrow + age	4	-67.10	142.51	4.12	0.03
day + marrow + elk + winter + age	6	-64.95	142.54	4.16	0.03
day + marrow + winter	4	-67.13	142.57	4.19	0.03
elk * marrow + day + age	6	-64.99	142.62	4.24	0.03
age * marrow + day + elk + winter	7	-64.17	143.20	4.82	0.02
age * marrow + day	5	-66.91	144.28	5.89	0.01
elk * age + day + marrow + winter	7	-64.71	144.28	5.90	0.01

Supplementary Table 3. Model selection results of factors affecting the probability of a wolf-killed adult male elk (≥ 5 years old) being a pedicled individual. We evaluated the effects of day in March (day), elk age (age), elk femur marrow percent fat (marrow), elk abundance (elk), and winter severity (winter). Models were developed using 139 wolf-killed male elk detected from 2004 – 2016. Models with a $\Delta AIC_c < 6$ are displayed. See Supplementary Fig. 8 for non-standardized and standardized beta coefficient estimates for models within 4 ΔAIC_c units of the top model.

References

- 1 Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S. & Evans, S. B. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management* **68**, 153-166 (2004).
- 2 Martin, H. W. *et al.* Factors affecting gray wolf (*Canis lupus*) encounter rate with elk (*Cervus elaphus*) in Yellowstone National Park. *Canadian Journal of Zoology*, doi:10.1139/cjz-2017-0220 (2018).
- 3 Kamischke, E. *Estimation of Kill Rates by Yellowstone Wolves*, Michigan Technological University, (2007).
- 4 Tallian, A. *et al.* Predator foraging response to a resurgent dangerous prey. *Functional Ecology* **31**, 1418-1429 (2017).