Wolf–Deer Movement After the 2021 Wolf Harvest, by North-South Gradient and Proximity to Towns using a Five-County Camera Record (2018–2025)

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Preprint — manuscript in preparation. 3 August 2026.

Abstract

Previous analysis of a wolf-enriched extract of the Snapshot Wisconsin camera network for five northwestern counties (Barron, Burnett, Bayfield, Douglas, and Sawyer; 525 cameras, 294,031 camera-days, 634,214 detections, 2018–2025; 1,856 wolf detections on 197 cameras) established patterns in the way gray wolves (*Canis lupus*) follow, select which class of deer to follow, and how strongly they displace white-tailed deer (*Odocoileus virginianus*). Using the same directional-following and return-interval methods, I asked whether the wolf–deer relationship differs (i) before versus after the February 2021 Wisconsin wolf harvest, (ii) near versus far from human development (per-camera Global Human Modification, GHM), and (iii) along a north–south latitude gradient. Then I asked how long a wolf delays returning to a camera after a person. Wolves arrived after deer 55% of the time before the harvest (n = 40), indistinguishable from a day-reassignment null (P = 0.30), and 85% after (n = 76, P = 0.002). The difference survived a joint model holding development and latitude fixed (odds ratio 4.8, P = 0.001) and a control that subsampled post-harvest wolves to the pre-harvest count (follow fraction 0.85, 95% band 0.75–0.94; no draw reached 0.55). Deer displacement by wolves was strongest in wild country and weakest near towns (wild ≈ 2.4×, most-developed cameras 1.5×; rank correlation P = 0.036). This was a nonlinear, threshold-shaped effect carried mainly by does (1.65× near vs 2.50× far, P = 0.058). Bucks stayed away from wolves more strongly than does, and did so everywhere, near towns and in wild country alike, so the easing near towns was a doe effect, not a buck one. Latitude was not an independent driver for the deer. The wolf's own avoidance of people was the largest of the three main relationships (2.78× its baseline revisit interval, 89 cameras, P < 0.0001) — greater than the deer's delay after a person (1.83×) or a wolf (2.24×). The wolf's avoidance of people was stronger after the harvest (joint model ×2.6, P = 0.009), independent of nearness to human development, and stronger in the southern counties (×0.6 per standard-deviation northward, P = 0.008). Actual following times were short and stable across every split (medians 3.8–7.0 min, no significant difference), indicating that what varied was how often wolves followed and how long deer stayed away, not the timing of the following. I interpret these patterns cautiously given the modest number of wolf encounters, and propose that analysis of a statewide wolf-enriched extract is the natural next step.

Keywords: camera trap; gray wolf; Canis lupus; white-tailed deer; Odocoileus virginianus; landscape of fear; human shield; wolf harvest; global human modification; predator–prey; Snapshot Wisconsin.

Introduction

Previous analyses of this five-county camera record showed that the regional wolf–deer relationship is shaped by season, by whether a deer is a buck or a doe, and by time of day. On shared trails wolves arrive after deer more often than chance would predict; among the nearest deer they approach antlered bucks more often than the bucks' numbers alone would predict; and they push deer away from a site more strongly than people do, while deer on one long-stewarded home ground return close to their normal schedule (Vraniak 2026a, 2026b). Those analyses pooled the whole record. That left questions unanswered — whether the same relationship holds evenly across time and space, and whether the wolf, until now treated only as the animal doing the following, is itself responding to people.

Three features of the record suggested the questions focused on in this report. First, the record spans the February 2021 Wisconsin wolf harvest — a season that took roughly 218 wolves in under three days and exceeded the state quota (Treves and Louchouarn 2022). If a harvest changes how wolves use the landscape, a record that straddles it should show the change. Second, every camera carries a Global Human Modification value (GHM), a 0-to-1 measure of how built-up its surroundings are — development, roads, and converted land (Kennedy et al. 2019). The cameras therefore run in an unbroken gradient from wild country to the developed edge of towns. This is the axis along which two long-standing ideas predict that predators and prey should rearrange themselves — the landscape of fear, in which prey avoid the places a predator makes dangerous (Laundré et al. 2001), and the human-shield hypothesis, in which prey shelter near people because predators avoid people (Berger 2007). Third, the five counties span about 126 miles from forested Lake Superior counties in the north to the farmland in the south — the same direction along which wolves recolonized the state (Wydeven et al. 2009).

Therefore, I asked four questions, using the prior study's methods. Does the wolf's following of deer, and how long deer stay away afterward, differ before and after the 2021 harvest? Do the following change with nearness to towns, or with latitude? And, applying the same "how long do they stay away" measure to the wolf itself: how long does a wolf wait before returning to a site after a person has passed? This last question is a direct test of whether the top predator itself behaves like prey toward people — the human "super predator" (Suraci et al. 2019; Kuijper et al. 2016). Because the number of wolf encounters is modest, I report these as extensions carrying certain uncertainties, not as settled effects.

Materials and methods

Dataset and validation

The data are the wolf-enriched five-county Snapshot Wisconsin extract described in the previous, parent study (Wisconsin DNR Office of Applied Science). Each detection record carries a species, date, time, and camera; each camera carries its survey effort in camera-days, a PLSS location (township, range, section), and a GHM value; and every deer is recorded as antlered (buck), antlerless (doe), or fawn. Before running any extension I rebuilt the parent pipeline from the raw files and confirmed that it reproduced the reported values exactly — 116 sequential wolf–deer encounters, a 0.75 follow fraction, a 5.8-minute median lag, and deer returning 2.24× and 1.83× more slowly after wolves and after people on 110 and 432 cameras. The splits below were run on the same, verified methods. Analyses were run in Python 3 (numpy, scipy, statsmodels).

Following and return-interval measures

Directional following is unchanged from the parent study. For each wolf detection, the nearest deer within 30 minutes was scored as *co-occurrence* (within 30 seconds), *follow* (the deer came before the wolf), or *precede* (the deer came after it). The follow fraction is *follow ÷ (follow + precede)*, where 0.50 means no consistent order. Significance comes from a 500-iteration day-reassignment permutation null, in which each wolf is reassigned to a random active day at the same camera and season, holding time of day fixed. The following time is the median deer-to-wolf lag on follow events. Displacement, or avoidance, is the per-camera ratio of the median return interval after a disturber to the responder's own baseline interval between detections (30-minute independence; a camera is kept only if it has at least three baseline gaps and three post-disturber returns). A ratio above 1.0 means the animal returns more slowly than usual (Creel and Christianson 2008 frame such delays as risk effects). I computed this ratio for deer after wolves and after people and — new here — for the wolf itself after people, using the same thresholds.

Splitting variables and models

Period before and after was split at 22 February 2021, the date of the harvest. Human development used the per-camera GHM value, analyzed three ways: as a median split, as thirds, and as a continuous covariate. Latitude used the PLSS township number (T31N–T52N). To tell these three influences apart, I fit joint models that hold the others fixed: a logistic regression of the per-encounter follow/precede outcome on period, GHM (z-scored), and township (z-scored) for the following signal, and ordinary least-squares regressions of the log return-interval ratio on the same predictors (HC3 robust errors) for the displacement measures. Between-group differences used Fisher's exact test (proportions), Mann–Whitney tests (ratio distributions), and Spearman rank correlations (continuous gradients). A Wilcoxon signed-rank test on the log ratio tested whether a delay exceeded 1.0. For the post-harvest jump in following, density control was added: the post-harvest wolf detections were subsampled down to the pre-harvest count (300 draws) and the follow fraction recomputed, to check whether the change was merely an artifact of the larger post-harvest wolf sample.

Results

Following before and after the harvest

The following signal was almost entirely a post-harvest one. Before 22 February 2021, wolves arrived after deer in 55% of 40 sequential encounters — no different from the day-reassignment null ($P = 0.30$). After the harvest, the fraction rose to 85% of 76 encounters ($P = 0.002$), and the two periods clearly differed (Fisher's exact $P = 0.001$). In a joint model that held nearness to towns and latitude fixed, the post-harvest odds of following were 4.8× higher ($P = 0.001$), while GHM and township added nothing ($P = 0.80$ and 0.60) and there was no interaction between period and development ($P = 0.58$). The density control confirmed that the jump is not a matter of sample size: subsampled to the pre-harvest count of 559 wolf detections, the post-harvest follow fraction stayed at 0.85 (95% band 0.75–0.94) across 300 draws, and not one draw fell to the pre-harvest value of 0.55 (Figure 1, Table 1).

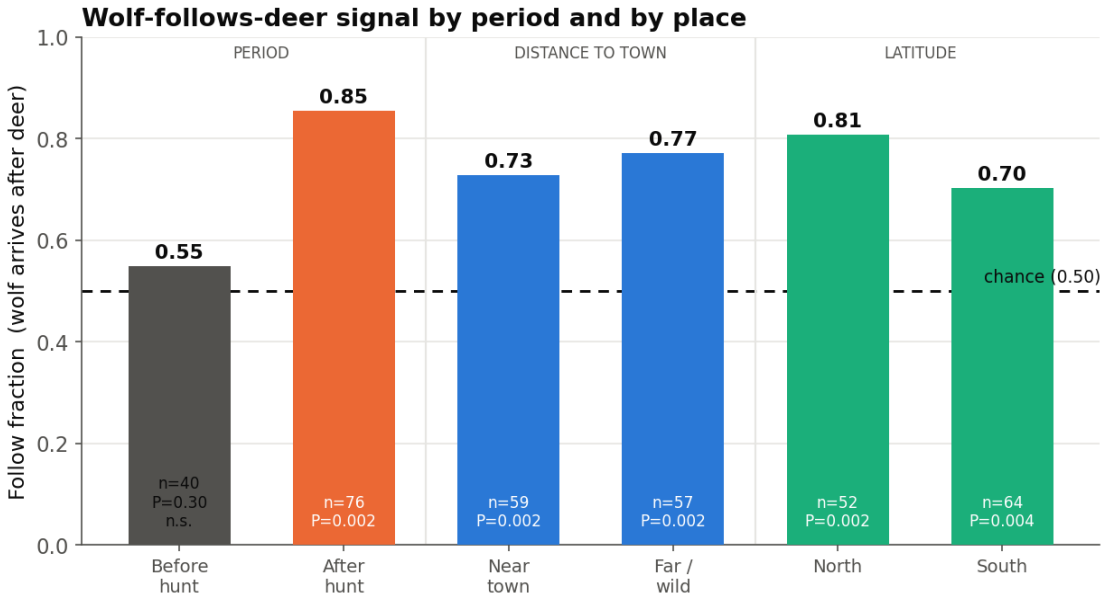

Figure 1. Follow fraction (wolf arrives after deer) by period and by place, against the day-reassignment null (0.50). Every group is significant except before the harvest; n and permutation P are shown on each bar.

Following across development and latitude, and following times

Across space, the following signal was uniform. Wolves followed deer at similar rates near towns and far from them (0.73 vs 0.77; both significant against their own nulls; between-group P = 0.67), and in the north and the south (0.81 vs 0.70; between-group P = 0.28). The following time itself — how far behind the deer the wolf arrived — was short and steady everywhere: medians of 3.8 to 7.0 minutes across all six subgroups, none differing significantly (all Mann–Whitney P > 0.2), close to the overall value of 5.8 minutes. What changed across period and place was therefore how often the wolf followed, and how long deer stayed away afterward not the timing of the follow itself.

Deer displacement across human development, and by deer class

How long deer stayed away after a wolf varied strongly with nearness to towns. Splitting cameras into thirds by GHM, deer returned 2.34× and 2.42× more slowly after a wolf in the wild and middle thirds, but only 1.49× more slowly at cameras located close to human development. Across all 110 wolf cameras this gradient was clear (Spearman r = −0.20, P = 0.036; median split P = 0.013). In plain time, deer in wild country took a median of about 55 hours to reappear after a wolf, against a roughly 21-hour baseline, whereas near towns they took about 19 hours against a roughly 14-hour baseline. The delay for deer returning after a person followed the same gradient more weakly (1.94× in wild country vs 1.75× near human development). The effect is not a smooth slope but a threshold — flat across proximity low and middle human development, and dropping only at the cameras closest to development — so a straight-line regression on GHM understated it (×0.88 per standard deviation, P = 0.41), even though the rank and thirds tests were clear. Latitude was not an independent predictor of how long deer stayed away (P = 0.59) (Figure 2).

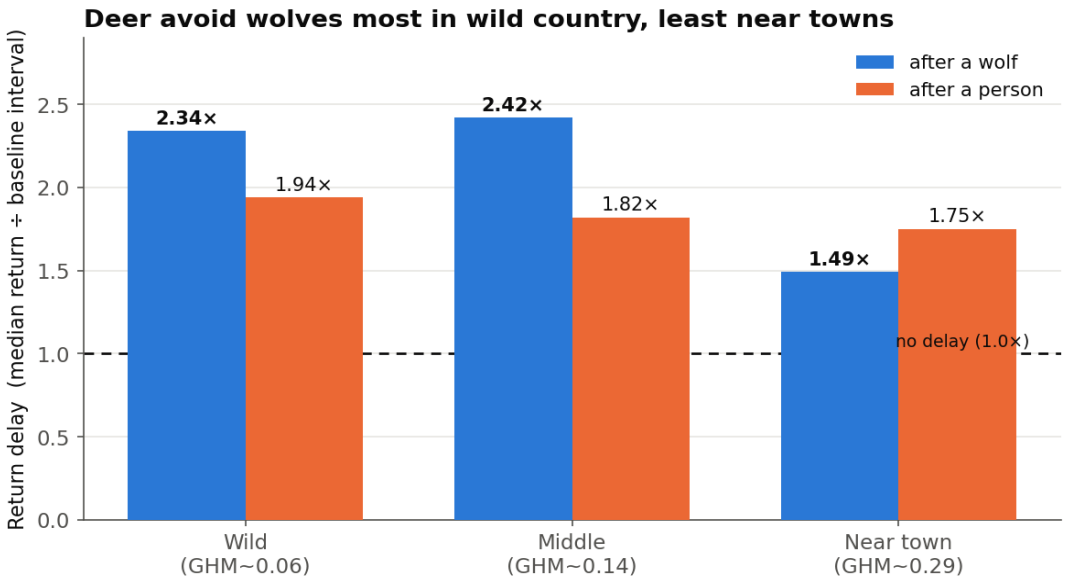

Figure 2. Deer return delay after a wolf (blue) and after a person (orange), by thirds of human modification. Baseline (1.0×) is the deer's own return interval.

Separating deer by class shows that the easing near towns was entirely a doe effect, and it also differentiated the movement of bucks and does. Two different things are being measured here: which deer a wolf tends to approach, and how long each kind of deer then stays away. The abundant, reliably detected does stayed away only briefly after a wolf near towns (1.65×), but strongly in wild country (2.50×; Mann–Whitney P = 0.058). This is the clearest class-level gradient, and it is what produces the overall easing of avoidance near towns. Bucks behaved very differently. They stayed away far longer than does in both settings — about 8.2× near towns and 11.9× in wild country, the difference between settings not significant. Rather than relaxing near people (Figure 3), a buck reacts to a wolf more strongly than a doe does, and does so wherever it is. Fawns resembled bucks. The buck and fawn ratios rest on sparse detections, so their exact size should be read with caution. The doe gradient is the most consistent single result. On the separate question of which deer the wolves approached, bucks remained over-represented as the nearest deer at every level of human development (selection ratio 1.95 near towns, 1.50 far), in line with the parent study's overall 1.84. In summary, wolves approach bucks more often than the bucks' numbers alone would predict, and bucks in turn stay away from a wolf longer than does do — while it is the does, not the bucks, whose return time response softens close to town.

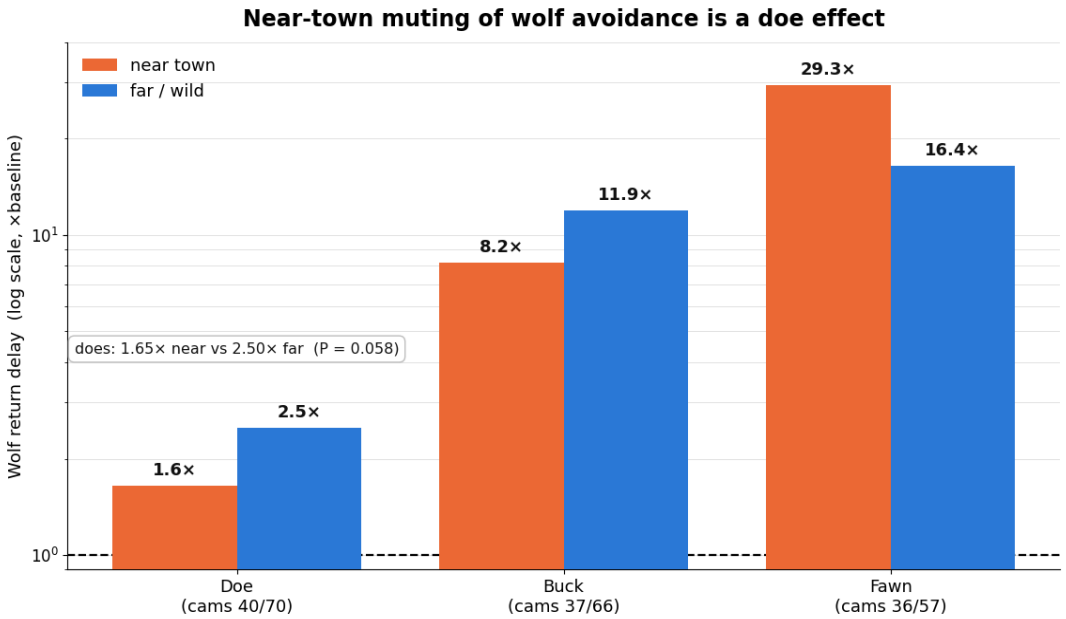

Figure 3. Wolf return delay by deer class, near town vs far/wild (log scale). The near-town reduction is a doe effect; buck and fawn ratios are noisy and rest on sparse detections.

The wolf's avoidance of people

Applying the same "how long do they stay away" measure to the wolf itself gave the largest response of the three main relationships. Across 89 cameras with enough wolf detections, wolves returned 2.78× more slowly after a person than on their own usual revisit schedule (Wilcoxon on the log ratio $P < 0.0001$) — a stronger reaction than the deer's delay after a person (1.83×) or a wolf (2.24×). This avoidance was stronger after the harvest (1.68× before, 3.40× after; joint model holding place fixed ×2.6, $P = 0.009$). It did not change with nearness to towns (3.22× near vs 2.57× far, $P = 0.96$; GHM continuum $P = 0.90$). And it was stronger in the southern counties (3.28× south vs 2.03× north; rank correlation with latitude $P = 0.012$; joint model ×0.60 per standard-deviation northward, $P = 0.008$), independent of human development (Figure 4, Table 2). Because a wolf revisits any single camera only every few weeks, the meaningful quantity is the ratio, not the absolute time. Relaxing the per-camera thresholds gave 107 cameras and a 1.91× median, in the same direction.

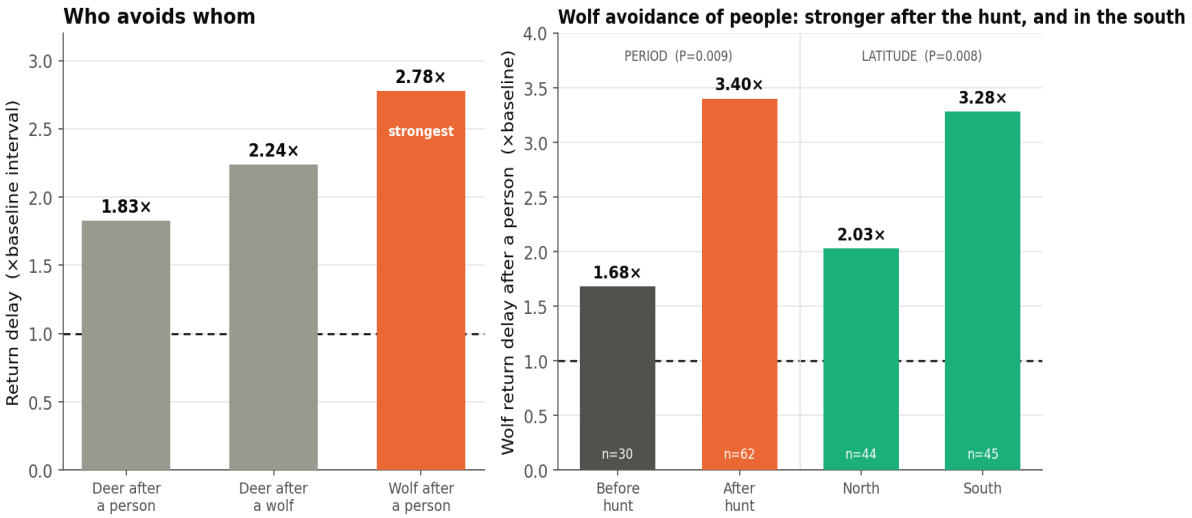

Figure 4. Left: return delay after a disturber across the three measurable relationships — the wolf's avoidance of people is the strongest. Right: the wolf's avoidance of people is stronger after the harvest and in the southern counties, and does not vary with distance to town.

Tables

Table 1. Directional following by group: follow fraction, sequential encounters (n), median following time, and one-sided day-reassignment permutation P.

Group	n	Follow fraction	Median lag (min)	Permutation P
Overall (validation)	116	0.75	5.8	0.002
Before harvest	40	0.55	3.8	0.30 (n.s.)
After harvest	76	0.85	5.9	0.002
Near town (high GHM)	59	0.73	7.0	0.002
Far / wild (low GHM)	57	0.77	4.5	0.002
North	52	0.81	5.9	0.002
South	64	0.70	5.0	0.004

Table 2. Return-interval ratios (return delay ÷ baseline). Deer responding to wolves and people, and the wolf responding to people; cameras in parentheses.

Group	Deer after wolf	Deer after person	Wolf after person
Overall	2.24× (110)	1.83× (432)	2.78× (89)
Before harvest	2.18× (44)	1.95× (223)	1.68× (30)
After harvest	1.68× (81)	1.77× (319)	3.40× (62)
Near town	1.58× (40)	1.75× (225)	3.22× (31)
Far / wild	2.48× (70)	1.97× (207)	2.57× (58)
North	2.29× (54)	1.89× (181)	2.03× (44)
South	2.05× (56)	1.77× (251)	3.28× (45)

Discussion

Understood together, these extensions of my previous study sharpen the parent study's picture, adding a new, who the predator is facing and where dimension to it. Two of the findings are robust, one is real but qualified, and one is essentially a negative result.

The clearest result is that two things intensified after the 2021 harvest: the wolf–deer following signal, and the wolf's own avoidance of people. The jump in following survives both a joint model and a density control, so it is not simply a by-product of the larger post-harvest wolf sample. And across the same divide the wolf's delay in returning after a person more than doubled. A harvest that exceeded its quota and killed a large fraction of the population in a matter of days (Treves and Louchouarn 2022) is a plausible occasion for heightened wariness, and the two behaviors move together in exactly the direction that a greater fear of people would predict — wolves keeping farther from human detections, while following deer trails more closely. This is an association, not a proven cause. The record grew and changed in other ways between 2018 and 2025 — deer abundance, the set of active cameras, the extent of wolf range — and only the most obvious of these, the larger number of wolves recorded afterward, has been controlled for here. Even so, the direction and size of the change make the harvest a hypothesis worth naming.

The human development gradient is the study's landscape-of-fear result. Deer stayed away from wolves for a long time in wild country but only briefly near towns, and that easing near towns fell on does rather than bucks. This is the pattern the human-shield hypothesis anticipates (Berger 2007; Kuijper et al. 2016) — where people crowd and habituate prey near development, the predator's added effect on how prey move shrinks, while in wild country the wolf dominates the deer's sense of risk (Laundré et al. 2001; Gaynor et al. 2018). That does relax near people while bucks stay wary everywhere fits the sex-based structuring of deer wariness found in the parent study and in the wider vigilance literature (Bowyer 2004; Lashley et al. 2014; Schuttler et al. 2017). A buck's response to a hunting-season landscape is not softened by being near a town, whereas a doe's tolerance of familiar human settings seems to extend to her response to the wolf. The effect is a threshold rather than a smooth slope — it appears only at cameras nearest human development— which is why it shows clearly in the rank and thirds tests but weakly as a straight-line term, and why splitting the thin wolf record by period and place at the same time exhausts its statistical power. Latitude added nothing on its own for the deer. The north–south contrast in the raw splits simply tracked the response to human development, because the northern counties are the less-modified ones.

The predator-facing measure — the wolf's own response to people — is the most striking single number in the study: the wolf was the most human-avoidant animal in the record, waiting longer to return after a person than deer waited after either people or wolves. This fits a growing body of work showing that large carnivores treat humans as a kind of super-predator and rearrange their movement around us (Suraci et al. 2019; Kuijper et al. 2016; Kudrenko et al. 2026). Two things set the wolf's avoidance of people apart from the deer's avoidance of wolves. First, it

ignored human development — wolves kept their distance from people whether near a town or deep in wild country. Second, it was patterned by latitude, stronger in the southern counties and independent of GHM. A plausible interpretation is range-edge history — the southern counties sit at the developed edge of Wisconsin's recolonized wolf range (Wydeven et al. 2009), where wolves are more recently established and have been more exposed to persecution, and where sharper wariness of people would be expected. This remains an interpretation. The wolf-as-responder measure is the most data-hungry in the study, resting on 89 cameras that thin to a few dozen once split.

The limits are those of the parent study, magnified by splitting the data. The following analysis rests on 116 encounters, and every partition thins it further. The displacement ratios are per-camera medians for an animal that visits any one camera rarely; and these are camera detections of unmarked animals, so "follow" and "return" describe the order and spacing of passages on shared trails, not the movements of tracked individuals. Therefore, these relationships can only be held so far. What supports confidence in the findings is their consistency of direction across several ways of cutting the data, and their fit with the landscape-of-fear and human-shield literature. The one change that would move them from suggestive to settled is more wolf encounters. A statewide wolf-enriched extract, built as the five-county one was and carrying the same fields — per-camera GHM, camera-day effort, and deer sorted into buck, doe, and fawn — would give the by-class, period-by-place, and continuous-gradient tests real power, widen both the development and latitude axes to their full range, and add encounters on both sides of the harvest. That is the natural next dataset I am pursuing.

Data and code availability

The five-county extract is drawn from the Snapshot Wisconsin citizen-science camera network (Wisconsin DNR, Office of Applied Science). The analysis pipeline extends the one reported in the parent study (Vraniak 2026b) and is held by the author and available on reasonable request. Exact localities of sensitive species are withheld for conservation reasons.

Acknowledgments

I thank Eli Wildey and the Wisconsin DNR Office of Applied Science for the wolf-enriched five-county extract designed with me, J. Stenglein for the Snapshot Wisconsin program, and A. Wydeven for review of the prior, parent analyses. This work draws on a long-term, family-stewarded prairie–savanna restoration and on the regional camera record of Snapshot Wisconsin.

Author contributions and disclosure

D.A.V. conceived the study, obtained and specified the Snapshot Wisconsin extract, directed all analyses, and is responsible for the content of this manuscript. Analysis was assisted by a large language model; all methods, statistics, results, and interpretations were specified, verified, and approved by the author, and the final text was written and edited by the author.

References

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3(6): 620–623. doi:10.1098/rsbl.2007.0415.

Bowyer, R. T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy 85(6): 1039–1052.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23(4): 194–201. doi:10.1016/j.tree.2007.12.004.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. Science 360(6394): 1232–1235. doi:10.1126/science.aar7121.

Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2019). Managing the middle: A shift in conservation priorities based on the global human modification gradient. Global Change Biology 25(2): 811–826. doi:10.1111/gcb.14549.

Kudrenko, S., Bischof, R., Zedrosser, A., Selva, N., … Heurich, M. (2026). Changes in wildlife activity patterns in response to war in Ukraine. Science 392(6804): 1282–1286. doi:10.1126/science.aed1493.

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proceedings of the Royal Society B 283(1841): 20161625. doi:10.1098/rspb.2016.1625.

Lashley, M. A., Chitwood, M. C., Biggerstaff, M. T., Morina, D. L., Moorman, C. E., & DePerno, C. S. (2014). White-tailed deer vigilance: the influence of social and environmental factors. PLoS ONE 9(3): e90652. doi:10.1371/journal.pone.0090652.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79(8): 1401–1409. doi:10.1139/z01-094.

Schuttler, S. G., Parsons, A. W., Forrester, T. D., Baker, M. C., McShea, W. J., Costello, R., & Kays, R. (2017). Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. Journal of Zoology 301(4): 320–327. doi:10.1111/jzo.12416.

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecology Letters 22(10): 1578–1586. doi:10.1111/ele.13344.

Treves, A., & Louchouarn, N. X. (2022). Uncertainty and precaution in hunting wolves twice in a year. PLOS ONE 17(3): e0259604. doi:10.1371/journal.pone.0259604.

Vraniak, D. A. (2026a). Quiet stewardship and deer return times: sound continuity, not fuel, predicts white-tailed deer avoidance of stewardship machines in a multi-year steward-conducted camera census. EcoEvoRxiv. https://doi.org/10.32942/X2V96R

Vraniak, D. A. (2026b). Gray wolves follow, select, and displace white-tailed deer across a five-county camera record. EcoEvoRxiv. https://doi.org/10.32942/X2XX09

Wisconsin Department of Natural Resources. (2018–2025). Snapshot Wisconsin. Wisconsin DNR Office of Applied Science, Madison, Wisconsin, USA.

Wydeven, A. P., Van Deelen, T. R., & Heske, E. J. (Eds.). (2009). Recovery of Gray Wolves in the Great Lakes Region of the United States: An Endangered Species Success Story. Springer, New York, USA.